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GEOPHILID CENTIPEDES: PHYLOGENY AND CHARACTER EVOLUTION

I GEOFILIDI (CHILOPODA): FILOGENESI ED EVOLUZIONE DI ALCUNI CARATTERI

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Introduzione

Chilopoda

I Chilopoda, una delle quattro classi dei Miriapodi, sono un importante gruppo di artropodi predatori diffusi in molti habitat terrestri, conosciuti in tutti i continenti eccetto in Antartide.

Comunemente sono noti come centopiedi, tuttavia sebbene il nome implichi il fatto che essi abbiano 100 piedi, essi presentano un numero di paia di zampe che varia tra 15 e 191, sempre in numero dispari.

Tutti i centopiedi presentano il primo paio di zampe modificato in un paio di forcipule che contengono le ghiandole velenifere. Infatti tutti i centopiedi sono quasi esclusivamente predatori, si nutrono di piccoli invertebrati infilzandoli con queste forcipule e iniettando loro il veleno; l'apparato boccale è costituito da mandibole e due paia di maxille, prime e seconde. La lunghezza totale del corpo varia tra 4 ai 300 mm (Edgecombe e Giribet, 2007); gli esemplari più grandi, principalmente scolopendre diffuse in zone tropicali, possono nutrirsi anche di vertebrati, come topi e lucertole, e il loro veleno può essere pericoloso anche per l'uomo, sebbene non siano stati registrati casi di morte nel mondo.

I chilopodi sono comunemente diffusi nel suolo, nella lettiera dal livello del mare fino alle zone di montagna. Solitamente sono predatori solitari, e molte specie cacciano soprattutto durante la notte.

Nonostante tutti i centopiedi siano costituiti da una testa e un corpo suddiviso in segmenti che portano un paio di zampe, esiste una notevole diversità all'interno del gruppo.

Le specie finora descritte sono circa 3300, ripartite in cinque ordini: Scutigeromorpha, Lithobiomorpha, Craterostigmomorpha, Scolopendromorpha e Geophilomorpha.

Gli Scutigeromorpha sono l'unico ordine che costituisce il gruppo degli Notostigmophora in contrapposizione ai Pleurostigmophora di cui invece fanno parte gli altri ordini: questa suddivisione è sostenuta da caratteri morfologici, in particolare dalla diversa organizzazione dell'apparato respiratorio, con aperture dorsali e brevi trachee che raggiungono il vaso dorsale (contenente emolinfa con un pigmento respiratorio) negli Scutigeromorpha (Notostigmofori) e aperture stigmatiche laterali e trachee ramificate in tutto il corpo negli altri Chilopodi (Pleurostigmofori) (Dohle 1985).

Le prime classificazioni dei chilopodi (Haase 1881, Attems 1926) raggruppavano gli ordini sulla base del tipo di sviluppo postembrionale:

Scutigeromorpha, Lithobiomorpha e Craterostigmomorpha hanno un tipo di sviluppo anamorfico (dal cui uovo esce un individuo con un numero di segmenti e paia di zampe che è inferiore a quello definitivo che sarà raggiunto solo con una serie di mute), mentre Scolopendromorpha e Geophilomorpha di tipo epimorfico (dalle cui uova, incubate dalla madre, esce un individuo con il numero definitivo di segmenti e paia di zampe).

Craterostigmomorpha, Scolopendromorpha e Geophilomorpha sono raggruppati nei Phylactometria, in cui la madre avvolge il proprio corpo attorno alle uova, primitivamente con il lato ventrale del corpo verso le uova (Edgecombe e Giribet, 2004).

Le scutigere (circa 100 specie) sono le uniche tra i chilopodi che presentano occhi composti, 15 paia di zampe molto lunghe, antenne come flagelli costituiti da moltissimi anelli; gli spiracoli si aprono dorsalmente sui tergiti; le madri depongono un singolo uovo nel terreno e alla schiusa presentano 4 paia di zampe, per arrivare poi al numero definitivo di zampe nel corso delle mute successive (sviluppo di tipo anamorfico).

I rappresentanti dell'ordine Lithobiomorpha (1100 specie riconosciute) presentano lo stesso numero di paia di zampe degli Scutigeromorpha; a differenza di questi ultimi però, l'apertura degli spiracoli non è dorsale, ma laterale, come i rappresentanti degli altri restanti ordini (detti nell'insieme Pleurostigmophora); presentano inoltre una testa appiattita dorso-ventralmente e delle antenne formate da un numero di articoli variabile tra i 15 e più di 100. Lo sviluppo post-embrionale è, anche in questo caso, di tipo anamorfico. Caratteristica peculiare dei litobi è la presenza di una serie di "speroni" sull'articolo basale dei gonopodi femminili e un ampio artiglio.

All'ordine dei Craterostigmomorpha appartengono due specie distribuite solo in Australia e Nuova Zelanda. Sono pleurostigmofori con 15 paia di zampe coperti da 21 tergiti, con alcuni segmenti coperti da due tergiti. Le antenne sono costituite da 17 -18 articoli; lo sviluppo post-embrionale è di tipo anamorfico: alla schiusa presentano 12 paia di zampe, le restanti vengono aggiunte durante le mute successive.

Gli ordini Scolopendromorpha e Geophilomorpha hanno uno sviluppo post-embrionale di tipo epimorfico: dalle uova esce un individuo con il numero definitivo di segmenti e paia di zampe.

Le scolopendre (più di 800 specie conosciute) sono tra i chilopodi i più aggressivi e i più voraci predatori; il numero di paia di zampe varia tra i 21 e i 23.

Geophilomorpha

Tra i chilopodi, i geofilomorfi sono l'ordine che presenta la maggiore diversità.

Si differenziano dagli altri chilopodi per il corpo molto allungato, il numero di segmenti che portano zampe varia da 27 a 191 e nella maggior parte delle specie è presente una certa variazione nel numero di segmenti tra gli individui e tra i sessi, con le femmine che tendono ad avere più zampe dei maschi. Il numero dei segmenti non varia durante la vita di un geofilomorfo.

Sono animali a sessi separati, ma il dimorfismo sessuale è poco sviluppato, solo in alcune specie nelle quali il maschio presenta l'ultimo paio di zampe più gonfie rispetto alle femmine.

Il corpo, tipicamente depresso, è costituito da una capsula cefalica ben differenziata, appiattita, di forma lenticolare, rettangolare o allungata. Su di essa si inserisce anteriormente un paio d'antenne di 14 articoli, relativamente corte circa 0,05 – 0,1 della lunghezza totale del corpo (Barber, 2009). Sono ciechi, ma possiedono organi meccanorecettori e chemorecettori a livello delle antenne, che permettono loro di orientarsi e di predare. Vivono in ambienti privi di luce, nella lettiera e nel suolo.

La parte anteriore della faccia ventrale della capsula cefalica è occupata dal clipeo, largo e ampio, che porta setae seguito dal labbro, la cui struttura è caratteristica delle famiglie, e, più indietro, dalle appendici boccali. Queste comprendono un paio di mandibole, un paio di prime mascelle e un paio di seconde mascelle.

Le mascelle prime si formano presumibilmente dalla fusione della coxa (segmento basale dell'appendice) con il rispettivo sternite, formando un coxosternite; presentano una coppia di telopoditi, proiezioni coxali e alcune volte due paia di palpi mascellari. Le mascelle seconde presentano un coxosternite solitamente non diviso, un telopodite formato da tre segmenti, l'ultimo dei quali è provvisto spesso di un'unghia, generalmente lunga e appuntita, a volte provvista di frange o di punte secondarie. Nel bordo posteriore del coxosternite vi sono i cosiddetti pori metamerici, aperture delle ghiandole coxali delle mascelle seconde.

Le appendici del primo segmento post-cefalico sono modificate in due forcipule, velenifere, che si muovono in senso latero-mediale e che sono usate per afferrare le prede ma, all'occorrenza, anche per difesa. Queste portano alla loro estremità un artiglio in cui sbocca la ghiandola velenifera.

Ciascuno dei segmenti del tronco pedifero è coperto da un tergite dorsale e uno sternite ventrale; su quest'ultimo si aprono di regola gruppi di pori (sbocchi di ghiandole unicellulari). Questi scleriti sono suddivisi trasversalmente in stretti pretergiti e presterniti, e larghi metatergiti e metasterniti, rispettivamente. I tergiti e gli sterniti sono connessi dalla membrana pleurale sulla quale sono differenziati altri piccoli scleriti (i pleuriti), che nei Geophilomorpha sono particolarmente sviluppati.

L'ultimo segmento del tronco vede la quasi totale assenza di pleuriti e presenta di regola un numero vario di pori coxali, alcuni aperti in fossette lungo lo sternite o il tergite e a volte nascosti. Le zampe dell'ultimo paio sono talvolta gonfie, soprattutto nei maschi, con una grande densità di setole nella regione ventrale; il tarso e metatarso sono separati e l'unghia terminale può essere rudimentale o assente.

Questi animali, come gli altri chilopodi, sono ovipari: le femmine depongono un piccolo numero di uova molto grandi e la fecondazione avviene attraverso il trasferimento indiretto di sperma per mezzo di spermatofore. Praticano cure parentali: le femmine rimangono avvolte a spirale attorno all'ovatura fino alla schiusa. Hanno sviluppo postembrionale di tipo epimorfico: i neonati, quando schiudono presentano già l'intero complemento di segmenti (Lewis, 1981).

Attualmente sono state descritte circa 1250 specie raggruppare in circa 215 generi (Bonato 2011), diffuse praticamente in tutto il mondo, eccetto Antartide e zona artica.

Correntemente sono riconosciute 13 famiglie*:* Aphilodontidae, Ballophilidae, Dignathodontidae, Eriphantidae, Geophilidae, Gonibregmatidae, Himantariidae, Linotaeniidae, Macronicophilidae, Mecistocephalidae, Neogeophilidae, Oryidae e Schendylidae (Bonato 2011).

Filogenesi

I chilopodi sono un gruppo monofiletico all'interno degli artropodi.

Ciascuno degli ordini dei chilopodi è riconosciuto come entità monofiletica supportata da analisi basate sia su dati morfologici che molecolari, considerati sia separatamente che in maniera integrata (Edgecombe e Giribet, 2007).

Gli scutigeromorfa occupano una posizione basale all'interno del gruppo dei Chilopoda (Notostigmophora) ed è sister group dei Pleurostigmophora (i restanti ordini).

All'interno dei Pleurostigmophora, i Craterostigmomorpha sono il sister group degli Epimorpha (Scolopendromorpha e Geophilomorpha) formando il clade Phylactometria. Quest'ultimi, a loro volta, sono il sister group del rimanente ordine dei Pleurostigmophora, cioè i Lithobiomorpha (fig.1) (Edgecombe, 2011).

Per quanto riguarda i Geophilomorphi in particolare, un primo contributo sulla loro filogenesi basato su caratteri morfologici, che include rappresentanti di tutte le famiglie conosciute, è Foddai & Minelli (2000).

L'integrazione di dati morfologici con dati molecolari ricavati dall'analisi di sequenze di DNA (Edgecombe et al. 1999, Giribet et al. 1999, Edgecombe & Giribet 2002, 2004, Giribet & Edgecombe 2006, Murienne et al. 2010) consolida la dicotomia basale tra i Placodesmata (con la sola famiglia Meci-stocephalidae, che presentano molti caratteri plesiomorfi) e gli Adesmata (le altre 13 famiglie).

I Mecistocephalidae sono il gruppo di geofilomorfi la cui filogenesi è maggiormente conosciuta con un'analisi cladistica dettagliata della famiglia in generale (Bonato et al. 2003), della sottofamiglia Arrupinae (Foddai et al. 2003) e del genere *Dicellophilus* (Bonato et al. 2009) in particolare. Tra gli Adesmata viene riconosciuta una relazione di stretta parentela tra Himantariidae, Ballophilidae e Schendylidae (Foddai e Minelli 2000), mentre la filogenesi interna di altre famiglie, in particolar modo quella dei Geophilidae, non è risolta.

I Geophilidae sono molto probabilmente un gruppo parafiletico che necessita ancora di una riclassificazione che in parte riveda l'attuale ripartizione in diverse famiglie (Geophilidae, Dignathodontidae, Aphilodontidae, Macronicophilidae e Linotaeniidae) di quelli che erano i Geophilidae, in senso ampio, nell'unica monografia complessiva a livello mondiale fino ad oggi pubblicata sul gruppo (Attems 1929).

Alle scarse conoscenze sulla filogenesi dei Geophilidae si contrappongono però i numerosi lavori tassonomici, orientati negli ultimi decenni soprattutto sui taxa delle zone temperate e delle regioni tropicali del Sud America (es. Pereira et al. 1995, 2000).

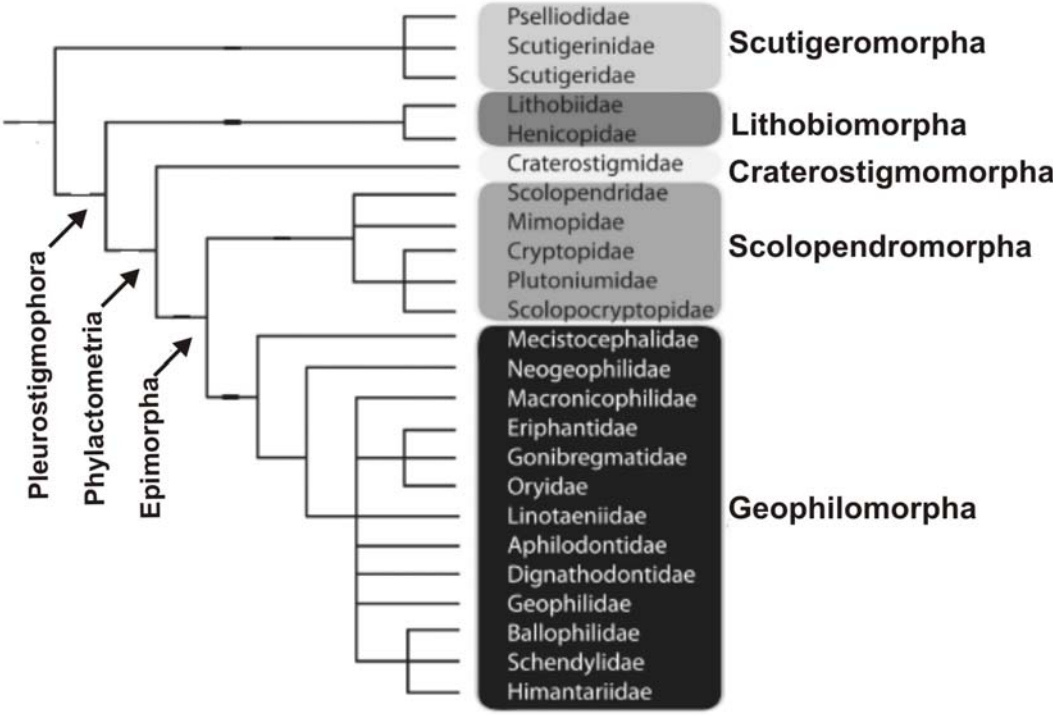

Fig. 1 Relazioni filogenetiche tra i Chilopoda (modificata da Edgecombe 2011)

Scopo

Lo scopo di questo lavoro è quello di cercare di ricostruire la filogenesi dei Geophilidae s.l. sensu Attems, sulla base dei caratteri morfologici esterni, per poi passare ad un'analisi comparata, all'interno dei Geophilidae stessi e, più in generale, dei Geophilomorpha, di alcuni caratteri particolarmente interessanti dal punto di vista ecologico: il calice velenifero che si trova, anteriormente, nelle forcipule, e i pori coxali che si trovano nelle coxe dell'ultimo paio di zampe e che sono implicati nel bilancio idrico dell'animale.

Sulla filogenesi ottenuta su base morfologica (escludendo i caratteri relativi ai calici veleniferi e ai pori coxali), ho quindi ricostruito i cambiamenti evolutivi di questi caratteri. Questo ha permesso di ricostruire le principali transizioni evolutive nell'evoluzione di questi caratteri, anche valutando ipotesi di convergenza e inerzia filogenetica.

Metodi

L'analisi filogenetica dei geofilidi è stata condotta su caratteri relativi alla morfologia esterna raccolti tramite microscopia ottica. La matrice di caratteri così ottenuta è stata analizzata in TNT (tree analysis using new technology; Goloboff et al. 2003) e in MrBayes (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003).

Per lo studio comparato di calice velenifero e pori coxali è stato necessario utilizzare un ulteriore protocollo, che prevede la digestione delle parti di interesse di alcuni esemplari e l'utilizzo di diverse tecniche di microscopia, il microscopio a contrasto di fase e il microscopio confocale a scansione laser, che sfruttando l'autofluorescenza della cuticola, permettono di rilevare queste strutture senza dover ricorrere a dissezioni.

La tesi si articola nelle tre parti di seguito descritte.

Manoscritto I- Filogenesi su base morfologica dei Geophilidae s.l. (Chilopoda: Geophilomorpha)

In questo manoscritto si è cercato di ricostruire la filogenesi dei Geophilidae s.l., documentando la diversità dei caratteri morfologici esterni che presentano maggiore diversità. Ho preso in considerazione 40 specie di cui 34 incluse come ingroup e appartenenti alla famiglia dei Geophilidae propriamente detta e alla famiglia dei Linotaeniidae, che le più recenti, ancorché parziali, analisi filogenetiche indicano con insistenza come un gruppo interno alla radiazione dei Geophilidae. Le restanti 6 specie (un rappresentante dei Mecistocephalidae, un Neogeophilidae, un Himantariidae, un Ballophilidae, uno Schendylidae e un Dignathodontidae) sono state invece utilizzate come outgroup.

I caratteri relativi alla morfologia esterna ritenuti utili per l'analisi filogenetica sono stati testati per la loro stabilità per quanto riguarda il dimorfismo sessuale e la variabilità intraspecifica e successivamente è stata costruita una matrice di 139 caratteri successivamente analizzata con i software per l'analisi filogenetica TNT e Mr Bayes. Ogni software di analisi è stato utilizzato per ciascun outgroup: in questo modo tutti gli outgroup sono stati testati separatamente.

Nelle analisi effettuate con outgroup diversi e con software diversi la topologia degli alberi ottenuti non cambia: vengono confermati sempre gli stessi cladi, supportati dagli stessi caratteri.

Alcune affinità tra generi concordano con la sistematica tradizionale: per esempio, è ben supportato il gruppo monofiletico costituito da *Stenotaenia linearis, Tuoba poseidonis* e *Clinopodes flavidus* (un tempo inclusi in un unico genere, *Clinopodes*).

Per quanto riguarda il genere *Geophilus*, i cui sette rappresentanti studiati formano effettivamente un clade, si può notare una relazione tra *Geophilus truncorum* e *Geophilus richardi*, un tempo attribuiti entrambi al genere *Brachygeophilus* Brolemann 1909; questi ultimi due costituiscono un gruppo monofiletico con *G. carpophagus*, mentre *G. alpinus, G. flavus e G. osquidatum* mostrano una certa affinità tra loro, in particolare il clade *G. flavus* + *G. osquidatum* è supportato da un alto valore di bootstrap.

Un altro clade riconoscibile è *Polygonarea sp.* + *Schendyloides alacer + Alloschizotaenia minuta* + *Hyphydrophilus adisi* + *Ribautia ducalis* + *Ribautia centralis,* che concorda con la classificazione di Attems (1929) che collocava tutte queste specie all'interno della sottofamiglia dei Chilenophilidae. *Plateurytion tenebrosus*, *Steneurytion antipodum* costituiscono un altro clade monofiletico così come *Pachymerium ferrugineum* e *Polycricus* sp.: quindi i rappresentanti delle antiche sottofamiglie Chilenophilinae e dei Pachymeriinae (Attems, 1929) costituiscono uno o due gruppi monofiletici. I Linotaeniidae sono un gruppo monofiletico, all'interno del quale si nota un'alta affinità tra *S. maritima* e *S. acuminata*.

È interessante notare come la posizione di *Zelanophilus provocator*, attualmente incluso nella famiglia Geophilidae, cambi utilizzando i diversi outgroup, mentre in tutte vengono sostanzialmente confermate le stesse relazioni tra la maggior parte delle rimanenti specie.

Zelanophilus provocator risulta avere una posizione basale ai Geophilidae s.l. considerando come outgroup i rappresentanti di quelle famiglie che sono ormai riconosciute essere alla base della filogenesi dei Geophilomorpha (*Dicellophilus*, rappresentante dei Placodesmata, e

Neogeophilus che presenta molti caratteri in comune con i Mecistocephalidae che lo collocano alla base del gruppo degli Adesmata). Numerosi caratteri, ad esempio il labbro costituito da due alae e dotato di dente mediano, e l'isolata distribuzione (Australia e Nuova Zelanda) suggeriscono che esso costituisca una famiglia a se stante, la cui collocazione filogenetica potrebbe trovarsi alla base degli altri Adesmata e lontano dai Geophilidae.

L'analisi filogenetica qui condotta risulta essere la più esaustiva delle filogenesi finora prodotte per la famiglia Geophilidae s.l., per quanto riguarda il numero dei generi presi in considerazione (23 generi in totale a fronte dei soli 5 generi considerati nel lavoro di Foddai e Minelli, 2000). Sia l'analisi di massima parsimonia che quella bayesiana, confermano l'ipotesi che il gruppo dei Geophilidae sia parafiletico, se in esso non si fa nuovamente rientrare il taxon Linotaeniidae, recentemente separatone come famiglia distinta.

Manoscritto II- Il calice velenifero nei Geophilomorpha (Chilopoda): morfologia comparata ed evoluzione

Questo manoscritto descrive la morfologia comparata e l'evoluzione di un carattere ad elevata specificità funzionale come il calice velenifero di un campione di specie di alcuni geofilomorfi.

Dal calice velenifero proviene il secreto che questi animali emettono attraverso un poro che si apre in vicinanza dell'apice delle forcipule. Il veleno così prodotto serve per uccidere o immobilizzare la preda.

Dall'analisi comparata delle specie prese in esame, il calice velenifero varia tra le specie sia per forma che per collocazione all'interno del segmento forcipulare: in alcune specie esso si colloca all'interno del tarsungulo, in altre nella tibia o nel femore o nel trocanteroprefemore del segmento forcipulare (rispettivamente terzo, secondo e primo articolo del segmento forcipulare), in altri casi si estende fino al coxosterno forcipulare, fino ad arrivare al caso eccezionale di *Henia vesuviana*, in cui il calice si colloca addirittura nel tronco dell'animale, fino al 27° segmento.

Una notevole diversità è stata riscontrata anche nella posizione del dotto del calice velenifero che non sempre decorre in modo rettilineo, ma può presentare delle curvature soprattutto nella parte terminale verso il calice. In tutte le specie analizzate il dotto decorre in prossimità del margine esterno del tarsungulo per poi rientrare, prima dell'altezza del calice, più o meno al centro del segmento forcipulare.

Anche per quanto riguarda la forma del calice velenifero, è stato possibile riconoscere una notevole diversità: si trovano calici simmetrici di forma cilindrica, con numerosi piccoli pori o con pochi pori distribuiti lungo il dotto; calici con pori concentrati solo alla base, con una forma più o meno arrotondata, ma non sempre simmetrica, a goccia, simmetrici, sub-cordati, non sempre simmetrici, di forma scampanata con il calice non simmetrico.

Mappando i caratteri sulla filogenesi ottenuta e utilizzando come outgroup un rappresentante degli Scolopendromorpha, sister-group dei geofilomorfi, è stato possibile trarre alcune considerazioni, la forma cilindrica risulta essere la condizione primitiva; questo carattere cambia tre volte almeno: c'è una transizione da forma cilindrica a forma arrotondata del calice velenifero, una transizione dalla forma arrotondata alla forma sub-cordata e una terza dalla forma arrotondata a una scampanata. Un caso particolare è rappresentato dalle tre specie prese in esame del genere *Henia*: il calice velenifero di *Henia vesuviana*, già stata documentata da Duboscq (1896), si trova nel tronco dell'animale e si estende fino al 23° segmento; i calici di *Henia bicarinata* e *Henia illyrica* invece sono collocati, rispettivamente, all'altezza del terzo e secondo articolo e del primo articolo del segmento forcipulare.

In base alle conoscenze desunte dalla letteratura riguardo gli habitat delle specie prese in considerazione, si è andati a vedere se in un determinato ambiente prevalesse una particolare forma di calice velenifero a discapito di un altro; tuttavia la forma e la posizione del calice velenifero nelle specie esaminate non sembra essere correlato al tipo di ambiente in cui si trovano le specie analizzate.

Manoscritto III- Organi coxali nei Geophilomorpha (Chilopoda): morfologia comparata ed evoluzione

In questo manoscritto vengono descritti i pori coxali tramite un' analisi comparata di 15 specie di Chilopoda Geophilomorpha.

I pori coxali si trovano nelle coxe dell'ultimo paio di zampe e che sono implicati nel bilancio idrico dell'animale e sono un carattere particolarmente interessante dal punto di vista ecologico: infatti, essi hanno funzione di osmoregolazione, espellendo acqua in condizioni umide e assorbendola in ambienti secchi (Rosenberg e Seifert, 1977). Voigtländer (2011) considera l'umidità come il più importante dei fattori abiotici responsabili della distribuzione dei centopiedi.

Lo studio delle specie considerate ha messo in evidenza una grande varietà per quanto riguarda il numero, le dimensioni e la disposizione sulle coxe dei pori coxali. Essi possono essere numerosi, distribuiti in modo diffuso sulle coxe sia dorsalmente che ventralmente, oppure solo ventralmente; in altre specie, invece, i pori coxali sono ridotti nel numero e distribuiti solitamente solo lungo il margine adiacente al metasternite; in altri casi, non si aprono direttamente sulla superficie della coxa, ma confluiscono in una o più tasche che si aprono sulla coxa o verso il confine di questa con il metasternite.

I canali dei pori coxali variano sia per profondità che per forma: possono essere cilindrici, o tozzi, quindi più o meno profondi con i lati del canale paralleli per tutta la lunghezza, oppure i lati possono essere arrotondati verso la parte terminale del canale, con la parte basale meno larga del diametro dell'apertura del poro; in altri casi, quando la fuoriuscita del poro non è diretta, ma diversi pori confluiscono in tasche, il canale, i cui lati corrono parallelamente per la maggior parte della lunghezza, presenta un restringimento verso la fine del poro, per poi allargarsi nuovamente alla base che risulta essere arrotondata e con un diametro minore rispetto all'apertura.

Dal punto di vista filogenetico, la forma primitiva dei pori coxali risulta essere quella con molti pori sparsi che si aprono direttamente sulla coxopleura; questo carattere cambia due volte; c'è una transizione a una condizione in cui i pori coxali si aprono in tasche sia sulla coxopleura sia lungo il margine del metasternite e una in cui i pori coxali sono aggregati e si aprono verso il margine del metasternite.

Il numero e la disposizione dei pori nelle coxe sono molto probabilmente correlati ai diversi ambienti colonizzati dalle specie analizzate.

Bibliografia

Si veda "references" a pag. 19.

Introduction

Chilopoda

The Chilopoda, one of the four classes of myriapods, are an important group of predatory arthropods common in many terrestrial habitats, known from all continents except Antarctica.

They are commonly known as centipedes, however, although the name implies that they have 100 feet, they have a number of pairs of legs, which varies between 15 and 191, always odd.

All centipedes have the first pair of legs modified into a pair of forcipules containing the venom glands. In fact, all centipedes are almost exclusively predators, feeding on small invertebrates with these forcipules, injecting them with venom. The mouthparts are represented by the mandibles and the second and first maxillae.

The total body length ranges from 4 to 300 mm (Edgecombe and Giribet, 2007). The largest species, mainly scolopendromorphs of tropical regions, may also feed on vertebrates such as mice and lizards, and their venom can be dangerous even for humans, although deaths were no recorded.

The Chilopoda are commonly found in soil and litter from sea level up to mountain areas. Usually they are solitary predators, and many species hunt mainly in the night.

Despite their similar basic body plan, centipedes are quite diverse. The 3300 species described are divided into 5 orders: Scutigeromorpha, Lithobiomorpha, Craterostigmomorpha, Scolopendromorpha, Geophilomorpha.

There is a basal division of Chilopoda into Notostigmophora (Scutigeromorpha) and Pleurostigmophora (all the other orders) (Dohle 1985); this split is supported by morphological characters, in particular by the different organization of the respiratory system: in Scutigeromorpha (Notostigmophora) there are tracheal lungs opening at spiracles on the posterior part of the tergites, while in all other chilopods (Pleurostigmophora) the spiracles open above the leg bases, at the sides of the body.

Haase (1881) and Attems (1926) divided Chilopoda in Anamorpha vs. Epimorpha according to the postembryonic development; anamorphic species add segments after hatching (Lithobiomorpha, Scutigeromorpha and Craterostigmomorpha), whereas epimorphic groups hatch with the complete adult number of segments (Scolopendromorpha and Geophilomorpha).

The maternal care of the eggs and hatchlings (the mother guarding the egg cluster by wrapping her body around it, primitively with the ventral side of the body against the egg) unite Craterostimomorpha with Epimorpha in the group of Phylactometria (Edgecombe and Giribet, 2004).

The scutigeromorphs (ca 100 species) are the only centipedes with compound eyes, 15 pairs of legs very long, whip-like antenne; the spiracles open dorsally on tergites; mothers lay a single egg in the lay. Hatchlings have 4 pairs of legs and the number of legs pairs grow in number until the adult stage (anamorphic development).

The Lithobiomorpha (ca 1100 recognized species) have the same number of pairs of legs as the Scutigeromorpha; they have their spiracles located on the side of the body (Pleurostigmophora); have a head flattened dorso-ventrally and the antenna consist of a number of articles ranging from 15 to over 100. They have an anamorphic post-embryonic development.

Only two species belong to the order of Craterostigmomorpha distributed in Australia and New Zealand. They are Pleurostigmophora with 15 pairs of legs covered by 21 tergites, with some segments covered by two tergites. The antennas consist of 17-18 articles; the postembryonic development is anamorphic type: hatching have 12 pairs of legs and the others are added during the subsequent growth.

The remaining two orders, Scolopendromorpha and Geophilomorpha have a epimorphic post-embryonic development: the juvenile leave the egg with the final number of segments and pairs of legs.

The scolopendromorphs (more than 700 species) are among the most aggressive and most voracious predators, the number of pairs of legs varies between 21 and 23, except for *Scolopendropsis duplicata* in which the number of legs pairs is 39 or 43.

Geophilomorpha

Among the Chilopoda, the geophilomorphs are the order with the greatest diversity.

They differ from the other Chilopoda for the very long body, the number of segments that varies from 27 to 191 and within each species there is usually variation in the number of segments between individuals and between sexes, with females having more legs than males.

The number of segments does not change during the post-embryonic life.

Geophilomorphs have separate sexes. Sexual dimorphism is in the last legs of male, more swollen than those of female.

The head, typically depressed, is covered by a cephalic capsule with a flattened, lenticular, rectangular or oblong shape.

The antennae are of 14 articles, relatively short, about 0.05 to 0.1 of total body length (Barber, 2009).

Geophilomorphs are blind, but possess mechanoreceptors and chemoreceptors in the antennae, which allow them to orient themselves and to catch prey in dark environments, in the litter and the soil.

The front of the ventral side of the cephalic capsule is occupied by the clypeus, broad and wide, carrying setae, followed by the lip, whose structure is characteristic of the families, and, further back, by the mouth-parts.

These include a pair of mandibles, a pair of first maxillae and a pair of second maxillae. The coxae of the first maxillae is presumably fused with the corresponding sternite forming a coxosternite; these appendages have a pair of telopodites, coxal projections and sometimes two pairs of maxillary palps. The second maxille have a coxosternite usually not divided medially, the telopodite consists of three segments, the last, usually long and pointed, sometimes equipped with fringed ends. In the rear edge of the so-called coxosternite there are metameric pores, openings of the coxal glands of the second maxillae.

The appendages of the first post-cephalic segment are modified into two forcipules, which move latero-medially and are used to grasp prey but, if necessary, for defense.

Each of the segments of the trunk is covered by a dorsal tergite and a ventral sternite on which open groups of pores corresponding to the outlet of unicellular glands. These sclerites are divided transversely into narrow pretergites and presternites, and wide metatergites and metasternites, respectively.

The tergites and sternites are connected by the pleural membrane on which are differentiated other small sclerites (the pleurites), which are particularly developed in Geophilomorpha.

The last segment of the body is almost without pleurites and usually presents a various number of coxal pores, some open in pits along the metasternite, sometimes are hidden under it. The last pair of legs are sometimes swollen, especially in males, with a greater density of bristles in the ventral region, tarsus and metatarsus are generally separated and the terminal claw is often rudimentary or absent.

These animals, like the other Chilopoda, are oviparous: females lay a small number of very large eggs and fertilization takes place through indirect transfer of sperm through spermatophores. Geophilomorphs practice parental care: females are coiled in a spiral around eggs until hatching.

The post-embryonic development is epimorphic (Lewis, 1981).

About 1250 species Have been described grouped into approximately 215 genera (Bonato 2011), spread practically all over the world except Antarctica and the Arctic.

Currently 13 families are recognized: Aphilodontidae, Ballophilidae, Dignathodontidae, Eriphantidae, Geophilidae, Gonibregmatidae, Himantariidae, Linotaeniidae, Macronicophilidae, Mecistocephalidae, Neogeophilidae, Oryidae and Schendylidae (Bonato 2011).

Phylogeny

The Chilopoda are a monophyletic group.

Each of the five orders of Chilopoda is recognized as a monophyletic entity supported by analyses based on morphological and molecular data, considered both separately and integrated (Edgecombe and Giribet, 2007).

The scutigeromorphs occupy a basal position within the group of Chilopoda (Notostigmophora) and is sister group of the Pleurostigmophora (the remaining orders).

Within Pleurostigmophora, the sister group of Craterostigmomorpha are Epimorpha (Scolopendromorpha and Geophilomorpha) forming the clade Phylactometria. The Lithobiomorpha are the syster group of Phylactometria (Edgecombe, 2011) (fig.1).

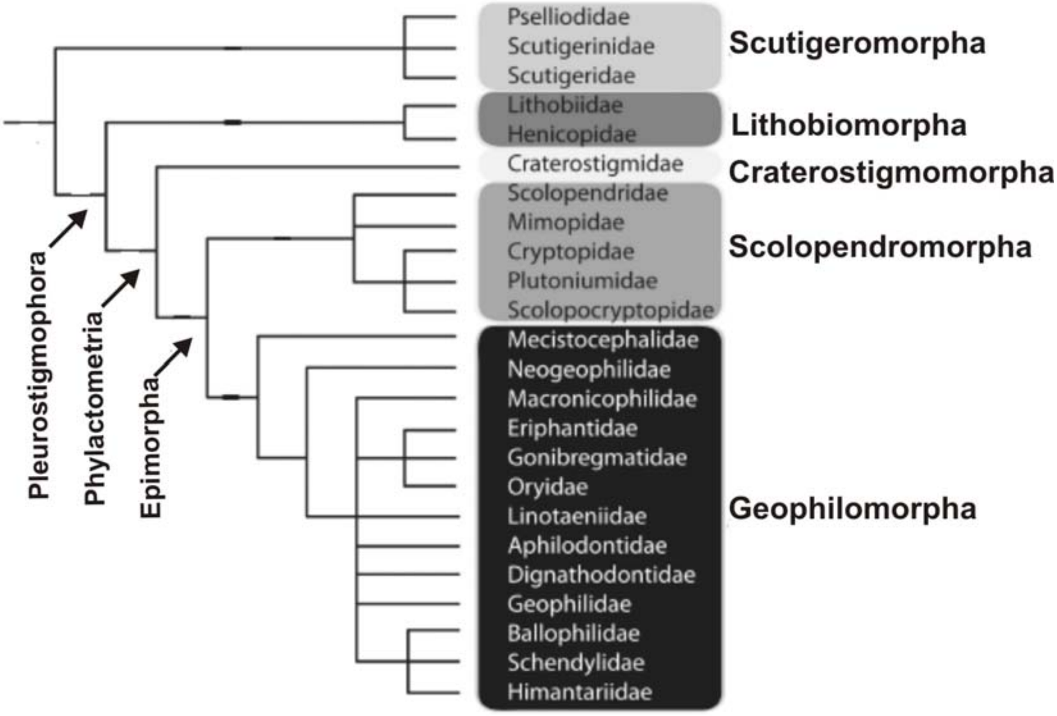

Fig. 1 Relationships of extant chilopod orders (modified by Edgecombe, 2011)

A first contribution to a phylogeny of Geophilomorpha based on morphological characters, which includes representatives of all known families, is Foddai & Minelli (2000).

The integration of morphological data with molecular data derived from the analysis of DNA sequences (Edgecombe et al. 1999, Giribet et al. 1999, Edgecombe & Giribet 2002, 2004, Edgecombe & Giribet 2006, Murienne et al. 2010) reinforces the basal split between Placodesmata (with the single family Mecistocephalidae, which have many plesiomorphic characters) and Adesmata (the other 13 families).

Among Geophilomorpha Mecistocephalidae is the family whose internal phylogeny is better known with more detailed cladistic analysis (Bonato et al. 2003), in particular the subfamily Arrupinae (Foddai et al. 2003) and the genus *Dicellophilus* (Bonato et al. 2009).

Among Adesmata there is a relationship of close phylogenetic affinity between Himantariidae, Ballophilidae and Schendylidae (Foddai and Minelli 2000). The internal phylogeny of the other families, especially the Geophilidae, is not resolved.

The Geophilidae are very probably a paraphyletic group that needs a reclassification. Recent studies unite back Geophilidae with Linotaeniidae (already included in the former according to Attems, 1929).

Questions adressed in this thesis

The aim of this work is to contribute to reconstructing the phylogeny of Geophilidae s.l. sensu Attems, based on external morphological characters, and to offer a comparative analysis, within the Geophilomorpha, of some characters of ecological importance: the poison calyx in the forcipules and the coxal pores on the coxae of the last pair of legs which are involved in the water balance.

Evolutionary changes of these characters (poison calyx and coxal pores) are reconstructed against the morphology-based phylogeny of the group.

Methods

The phylogenetic analysis of Geophilomorpha was conducted on characters related to the external morphology collected by light microscopy. The matrix of characters thus obtained was analyzed in TNT (tree analysis using new technology; Goloboff et al., 2003) and MrBayes (Huelsenbeck and Ronquist, 2001, Ronquist and Huelsenbeck, 2003).

For the comparative study of poison calyx and coxal pores it was necessary to use another protocol, which provides for the digestion of some specimens and using different techniques of microscopy (DIC and CSLM) taking advantage of the autofluorescence of the cuticle, and allows to detect structures without dissection.

The thesis is articulated into three parts as described below.

Manuscript I - A morphology-based phylogeny of Geophilidae s.l. (Chilopoda: Geophilomorpha)

In this manuscript I tried to reconstruct the phylogeny of Geophilidae s.l., documenting the diversity of external morphological characters. I took into account 40 species of which 34 are included in the ingroup and belong to the family of Geophilidae and to the Linotaeniidae that the most recent phylogenetic analyses repeatedly indicates as a group within the radiation of Geophilidae. The remaining 6 species (belonging to Mecistocephalidae, Neogeophilidae, Himantariidae, Ballophilidae, Schendylidae and Dignathodontidae) were included, instead, in the outgroup.

The characters of external morphology considered useful for phylogenetic analysis were tested for their stability with respect to the sexual dimorphism and intraspecific variability; then a matrix of 139 characters was made and analyzed with two software packages for phylogenetic analysis, TNT and Mr. Bayes.

All the outgroups were tested separately with each software; the topology of the trees thus obtained is the same: the clades were all confirmed and supported by the same characters.

Some similarities between genera agree with the traditional taxonomy: for example, a well-supported monophyletic group consisting of *Stenotaenia linearis, Tuoba poseidonis* and *Clinopodes flavidus* (in the past all included in only one genus, *Clinopodes*).

For the genus *Geophilus*, whose seven species studied all clustered as a clade, there was a closer relationship between *Geophilus truncorum* and *Geophilus richardi*, once both attributed to the genus *Brachygeophilus* Brolemann 1909; this clade forms a monophyletic group with *G. carpophagus*, while *G. alpinus, G. flavus* and *G. osquidatum* form another clade.

Polygonarea sp.+*Schendyloides alacer*+*Alloschizotaenia minuta*+*Hyphydrophilus adisi*+*Ribautia ducalis*+*Ribautia centralis* are grouped in a clade, which agrees with the classification of Attems (1929) who placed all these species in the subfamily Chilenophilinae. *Plateurytion tenebrosus* +*Steneurytion antipodum* constitute another monophyletic clade and *Pachymerium ferrugineum*+*Polycricus* sp. another one.

Therefore the representatives of the ancient subfamilies Chilenophilinae and Pachymeriinae (Attems, 1929) constitute one or two monophyletic groups.

The Linotaeniidae are a monophyletic group.

Interestingly, the position of *Zelanophilus provocator*, currently included in the family Geophilidae, changes using different outgroups. *Zelanophilus provocator* has a basal position in Geophilidae s.l. considering as outgroup representatives of those families that are now recognized to be at the base of the phylogeny of Geophilomorpha (*Dicellophilus*, representative of Placodesmata, and *Neogeophilus* which has many features in common with Mecistocephalidae that place it at the base of the group of Adesmata). Several characters, such as the two alae and the median tooth of the labrum and its isolated geographical distribution (Australia and New Zealand) suggest that it constitutes itself a family, whose phylogenetic position could be at the basis of the other and Adesmata away from Geophilidae.

The phylogenetic analysis conducted here is the most comprehensive phylogeny of the family produced for Geophilidae s.l., as regards the number of genera taken into account (23 genera in total compared with only 5 considered in the work of Foddai and Minelli 2000).

Both the maximum parsimony and the Bayesian analyses support the hypothesis that Geophilidae is a paraphyletic group, if Linotaeniidae (currently recognized as a distinct family) are excluded.

Manuscript II - The poison calyx of Geophilomorpha centipedes (Chilopoda): comparative morphology and evolution

This manuscript describes comparative morphology and evolutionary trends of a character with high functional specificity: the poison calyx of geophilomorphs.

The venom produced by centipedes is used to kill or immobilize prey.

The poison calyx varies between species both in form and position within the forcipular segment: in some species it is found in the tarsungulum, in others in the tibia or the femur or in trocanteroprefemor of the forcipular segment (respectively third, second and first articles of the forcipular segment), in other cases it extends to the forcipular coxosternum, or even in the trunk, as in exceptional case of *Henia vesuviana*, where the calyx is in the 27° trunk segment.

A significant difference was also found in the position of the poison duct: in some species it runs straight, in others not so. In all species analyzed the duct runs along the external edge in the distal part of the tarsungulum but it moves towards the middle in the proximal part of the tarsungulum.

Also the shape of the poison calyx varied among the species considered: symmetrical cylindrical, with numerous small pores or with a few scattered pores along the duct; or pores only concentrated at the base; more or less rounded shape, but not always symmetrical, drop-like, symmetrical, sub-chordate, not always symmetrical, bell-shaped non-symmetrical.

The phylogenetic position of taxa with different shape of poison calyx can be evaluated against the consensus phylogeny suggested by the morphological analysis performed with a scolopendromorph as outgroup: the cylindrical shape appears to be the plesiomorphic condition, and this character changes several times.

Based on knowledge derived from the literature about the habitats of species considered, I tested if a shape of poison calyx prevails in a particular environment, but I found no correlation between shape and habitat.

Manuscript III- Coxal organs in Geophilomorpha: comparative morphology and evolution

This manuscript describes the coxal pores through a comparative analysis of 15 species of Chilopoda Geophilomorpha. The coxal pores open on the coxae of the last pair of legs and are involved in the water balance of the animal: in fact, they have osmoregulatory function, expelling water under wet conditions and absorbing it in dry environments (Rosenberg and Seifert, 1977). Voigtländer (2011) considers the humidity as the most important abiotic factor responsible for the distribution of centipedes.

The study of these species showed a great diversity in terms of the number, size and arrangement of pores on the coxa. Pores can be numerous, widely distributed on both dorsal and ventral surface of the coxa, or only ventrally in other species, or the coxal pores are reduced in number and usually distributed only along the adjacent margin of the metasternite; in other cases they not open directly onto the surface of the coxa, but into one or more pits that open on the coxa.

The channels of coxal pores vary in depth and in shape: they can be cylindrical and more or less deep, with uniform diameter along the length, or the diameter is not uniform, in some species the channel narrows towards the deep end, especially in the coxal pores that open into pits.

The phylogenetic reconstruction with a scolopendromorph as outgroup identifies as the plesiomorphic condition many scattered deep pores that open directly on the coxopleura; this character changes twice in the species set I have investigated: there is a transition to a condition in which the pores open into pockets and one in which the coxal pores are aggregated and open to the edge of metasternite.

The number and arrangement of coxal pores is probably related to different environments colonized by the species analyzed.

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A morphology-based phylogeny of Geophilidae s.l. (Chilopoda: Geophilomorpha)

Abstract

Thirteen families are currently recognized within the geophilomorph centipedes, with a total of more than 1200 described species worldwide. A basal split between Mecistocephalidae (Placodesmata) and all other geophilomorphs (Adesmata) is supported both by morphological and molecular data. Within the Adesmata, a clade Geophilidae s.l. sensu Attems (1929) that includes the Geophilidae, Dignathodontidae, Aphilodontidae e Linotaeniidae of current classifications, is quite probably a nonmonophyletic group in need of reassessment. The present paper is an attempt at reconstructing the phylogeny of Geophilidae s.l. based on external morphology characters. Based on original light microscopy observations, I document here morphological variation in 40 species of Geophilomorpha, of which 35 belong to the ingroup Geophilidae s.l. and 5 are used as outgroups. The data matrix includes 139 morphological characters. Weighted parsimony was used for phylogenetic reconstruction and bootstrapping and branch support and bayesian analyses were performed to evaluate tree topology stability. Within Geophilidae s.l., some genera cluster into lineages which agree with traditional groupings proposed by Attems: we can recognize the clades corresponding to the subfamilies of Chilenophilinae+Pachymeriinae and Geophilinae, plus the 'Linotaeniidae' originally classified as subfamily Dignathodontinae together with only distantly related taxa. The placement of *Zelanophilus provocator* within the Geophilidae is questioned.

Introduction

Geophilomorpha is one of the main clades, traditionally classified as orders, forming the class Chilopoda together with Lithobiomorpha, Craterostigmomorpha, Scolopendromorpha and Scutigeromorpha.

The body of geophilomorphs is narrow and elongate (adult length from ca 1 cm to 22 cm), the color usually yellow to brown. Geophilomorphs differ from the other chilopods in the number of pairs of legs, which is from 27 to 191, whereas all other centipedes have either 15 or 21 or 23, to the exception of the recently described scolopendromorph *Scolopendropsis duplicata* Chagas, Edgecombe and Minelli 2008 (Chagas et. al. 2008). In geophilomorphs, segment number is often variable within each species and usually higher in females than in the conspecific males. These centipedes have epimorphic development, hatching with the complete adult number of segments. All species are blind. The head capsule is always flat but variable in shape; anteriorly it bears two antennae with a fixed number of articles (14). The ventral anterior part of the cephalic capsule is the clypeus, which bears a variable number of setae, also variously arranged. The mouth-parts include labrum, mandibles, and first and second maxillae. The labrum is variable in structure, often fringed by a row of denticles or bristles. The mandibles are mostly delicate, with the apical part very different in the different families: only a pectinate lamella (Geophilidae) or a series of pectinate lamellae (Mecistocephalidae and Oryiidae), a pectinate lamella accompanied by a series of dentate lamellae (Schendylidae), or a dentate lamella accompanied by a series of pectinate lamella (Himantariidae) (Bonato, 2011). The Geophilomorpha are almost exclusively predatory and the prey is immobilized by venom injected through the first pair of trunk appendages specialized as poisoning maxillipedes, the forcipules.

The anterior margin of the forcipular coxosternite is either smooth or bearing at most a pair of denticles; the forcipular telopodites are of four articles (trochanteroprefemur, femur, tibia and tarsungulum, in this order from the coxosternite to the ultimate article), often with teeth along the inner margin.

The dorsal sclerites (tergites) are divided into a shorter and narrower pretergite, and a rather long and broader metatergite. Ventrally the sclerites are called sternites, each of these divided in a short presternite and longer metasternite; the sternites usually are provided with ventral pores (Turcato et al. 1995), whose arrangement is of great taxonomic importance. Many geophilomorphs exhibit a "transition" between the anterior and posterior region of the trunk, the former bearing for example pit-and-socket structures (the so-called carpophagus structures), as in many Geophilidae; in other taxa, a "singularity" marks a few segments at ca. 37-45 % of the total number of segments, as in the case of the lateral virguliform fossae on some sternites of the himantariid *Stigmatogaster gracilis* (Meinert, 1870).

The legs are inserted ventrolaterally on the trunk segments. Each leg is constituted by 5 articles (i.e. trochanter, prefemur, femur, tibia and tarsus), with an apical claw called pretarsus. The ultimate legs are variously different from the other legs: a couple of pleurites are adjacent to the pretergite, and usually fused, forming a pleuropretergite, and the metatergite has a rounded posterior border. The presternite is usually constricted medially, whereas the metatergite is usually trapeziform, but variable in shape. The coxae of ultimate leg-bearing segment are usually swollen and contain the so-called coxal organs, in variable number, that open on the surface of the integument by means of pores, variably arranged on the coxopleura, or inside common pits. Number and arrangement of the coxal pores are diagnostic characters. The ultimate pair of legs are generally modified, and their function is not locomotory. These appendages are often sexually dimorphic, with swollen telopodite in the males; the tarsus is most often composed of two articles (tarsus 1 and tarsus 2), often ending in a terminal claw (pretarsus), otherwise missing or replaced by spines.

In the posterior part of the trunk, three segments are recognized by Brolemann (1930) and Lewis (1981): the intermediate segment, the first genital segment with a pair of gonopods, and the second genital segment with the penis or the vulva, followed by the telson with the anal valves.

In the females the gonopods are usually fused and very short. Male gonopods instead are bi-articulated, with a "penis" in between (Lewis, 1981).

A pair of anal organs is usually present.

During the whole brooding period, females coil around the egg clutch and the newly hatched juveniles with the sternites either inward (*Dicellophilus carniolensis* (Koch, 1847); Bonato and Minelli, 2002) or outward.

Geophilomorpha is the major centipede lineage with the greatest diversity and almost worldwide distribution, except for Antarctica and most Arctic regions. The taxon includes ca 1250 valid species in 13 families, ca 215 extant genera and three extinct genera.

Leach (1814) estabilished a separate taxon for these centipedes, by introducing the genus *Geophilus*. In 1895 Cook proposed a first classification in "families" of Geophilomorpha, using characters related to the mouth-parts (mandible, maxillae 1 e 2). Nine families were recognized: Gonibregmatidae, Oryidae, Himantariidae, Disargidae, Ballophilidae, Schendylidae, Dignathodontidae, Geophilidae, Dicellophilidae.

Detailed comparative analyses of character states were published by Brolemann and Ribaut (1912) for the Schendylidae, and by Chalande and Ribaut (1909) for the Himantariidae.

In the following years, other authors (Attems, 1903; Verhoeff, 1908; Brolemann, 1909) proposed new classifications.

In 1929, Attems published a monograph that represents the first and hitherto only complete taxonomic account of the entire order. Attems distinguished ten families: Himantariidae, Schendylidae (with 2 subfamilies Schendylinae e Ballophilinae), Oryidae, Mecistocephalidae, Geophilidae, Soniphilidae, Gonibregmatidae, Sogonidae, Neogephilidae and Azygethidae. Within the Geophilidae, he recognized the subfamilies Geophilinae (including the genera *Geophilus*, *Nesogeophilus*, *Orinophilus, Brachygeophilus*, *Galliophilus*, *Purcellinus*, *Mesogeophilus*, *Simophilus*, *Pleurogeophilus*, *Clinopodes*, *Geoporophilus*, *Pachymerellus*, *Insigniporus*, *Erithophilus*, *Leptophilus*, *Chalandea*, *Eurygeophilus*, *Australiophilus*, *Geoperingueya*, *Apogeophilus*, *Dinogeophilus*, *Nannocrix*, *Arenophilus*), Dignathodontinae (genera *Scolioplanes*, *Diplocora*, *Agathothus*, *Henia*, *Chaetechelyne*, *Dignathodon*, *Pagotaenia*), Pachymeriinae (including the genera *Pachymerium*, *Tasmanophilus*, *Eurytion*, *Schizotaenia*, *Sepedonophilus*, *Philogeonus*, *Pachymerinus*, *Geomerinus*, *Macronicophilus*, *Achilophilus*, *Maoriella*), Chilenophilinae (including the genera *Chilenophilus*, *Nesidiphilus*, *Suturodes, Ribautia*, *Arctogeophilus*, *Queenslandophilus*, *Polygonarea*, *Lestophilus*, *Taiyuna*, *Brachygonarea*, *Gnathoribautia*, *Proschizotaenia*, *Telocricus*, *Schizonampa*, *Watophilus*, *Alloschizotaenia*) and Aphilodontinae (including the genera *Aphilodon*, *Mecophilus*, *Philacroterium*, *Mecistauchenus*).

The classification of the Geophilomorpha given by Lewis (1981) was based on Attems (1929)'s arrangement, with the modofications of Crabill (1961, 1970) who proposed the synonymy of Azygethidae with Oryidae and added a new family, Eriphantidae; Lewis thus distinguished 11 families: Himantariidae, Schendylidae, Oryidae, Mecistocephalidae, Geophilidae including the Sogonidae of Attems (1929), Chilenophilidae, including the Pachymeriinae of Attems (1929), Eryphantidae, Dignathodontidae, Aphilodontidae, Gonibregmatidae and Neogeophilidae.

Currently, 13 families are recognized: Aphilodontidae, Ballophilidae, Dignathodontidae, Eriphantidae, Geophilidae, Gonibregmatidae, Himantariidae, Linotaeniidae, Macronicophilidae, Mecistocephalidae, Neogeophilidae, Oryidae and Schendylidae (Edgecombe and Giribet 2007, Bonato 2011).

Current knowledge on the morphology of geophilomorphs is uneven: detailed information is available for few species, whereas for most species only descriptions and illustrations of few taxonomically relevant characters are available; taxonomic work in the past 25 years has concentrated on these families: Schendylidae, Geophilidae (especially those from the temperate and tropical South America, e.g. Pereira et al. 1995, 2000) and Mecistocephalidae. Mecistocephalidae is currently the best understood geophilomorph group in terms of phylogeny, with detailed cladistic analysis of the family as a whole (Bonato et al. 2003) and the subfamily Arrupinae (Foddai et al. 2003) and the genus *Dicellophilus* (Bonato et al. 2010) in particular.

Many characters provide evidence for the monophyly of the order Geophilomorpha: eyes are lacking (all the species are blind); the antennal segment number is fixed at 14; on the terminal antennal article there are two lateral areas bearing sensilla; the mandibles are small and there is not mobility of the anterior tentorial arms; the number of leg-bearing segments is at least 27; the trunk is homonomous (no alternation of long and short tergites), with a spiracle on the all leg-bearing trunk segments except the last;

tracheal chiasmata (giving rise to moulting rings; Minelli, 1985); pleuron with a larger number of small pleurites than in the other “orders”; antennae and legs do not regenerate.

The phylogenetic relationships within the Geophilomorphs are still poorly known (Edgecombe & Giribet 2007), but ongoing work is rapidly improving it.

Morphological (Foddai 1998, Foddai & Minelli 2000) and molecular analyses (Edgecombe et al. 1999, Giribet et al. 1999) divide Geophilomorpha into two clades, the Placodesmata (composed of the single family Mecistocephalidae, which have many plesiomorphic characters) and Adesmata (all the other 13 families) (fig. 1).

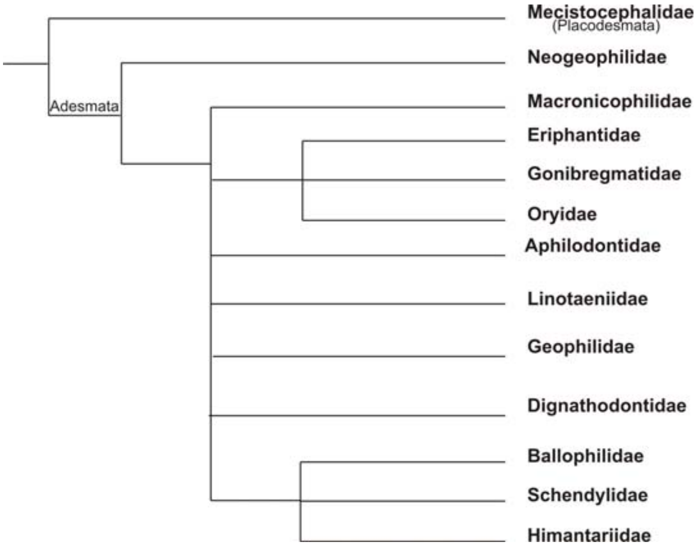

Fig. 1. Geophilomorpha phylogenetic relationship according to Foddai and Minelli 2000.

Published phylogenetic work on geophilomorphs is based on more than 190 characters of external anatomy (Foddai 1998, Edgecombe et al. 1999, Foddai and Minelli 2000, Edgecombe & Giribet 2002, 2004, Giribet & Edgecombe 2006, Murienne 2010); combined analyses of morphological and molecular data (analysis of DNA sequences, 18S and 28S rRNA, elongation factor 1 and 2, RNA polymerase II, 16SrDNA and cytochrome c oxidase I) (Giribet et al. 1999, Edgecombe & Giribet 2004, Giribet & Edgecombe 2006, Murienne et al. 2010), but it has not yet been used to reconstruct the morphological evolution of these animals.

The morphology-based phylogeny of Geophilomorpha by Foddai & Minelli (2000) remains the only work that includes exemplars of all 14 currently recognized families. The most densely sampled molecular analyses to date (Edgecombe & Giribet 2004, Murienne et al. 2010) include members of just 8 families. Molecular data are especially needed for the Eriphantidae, Eucratonychidae, Gonibregmatidae, Macronicophilidae and Neogeophilidae, most of which are not collected with regular frequency.

Within Adesmata, morphological and molecular data agree in grouping together Himantariidae, Ballophilidae and Schendylidae (Foddai & Minelli 2000, Edgecombe e Giribet 2004).

Geophilidae s.l. (sensu Attems, 1929) is evidently a paraphyletic group in need of reclassification. Recent studies unite back Geophilidae with Linotaeniidae (already included in the former Attems, 1929).

Member of the Geophilidae Leach, 1815 have body slender but variable in shape (fig. 2). The head is usually slightly or moderately elongate; antennae are slender. The labrum is often composed of a narrow intermediate part with tubercles and two wider lateral parts with bristles. The mandibles have only a single pectinate lamella. The second maxillae are variable. The forcipular segment is elongate and broad, with two paramedian sclerotized lines on the coxosternum. The number of leg-bearing segments is variable within each species. Sternal pores are often present and not always arranged in the same pattern along the trunk; the species-specific arrangement is a diagnostic character. Coxal organs are usually present, opening either in distinct pores or in pits. The female gonopods are usually an undivided lamina. Ca 560 species in ca 100 genera are currently recognized. Geophilidae are distributed almost worldwide, to the exclusion of Antarctica and some areas in western Africa and southern and south-eastern Asia. Maximum diversity and richness are in the south-western part of North America and in southern Europe; a high number of species is also found in South America, southern Africa and Australasia (Bonato 2011).

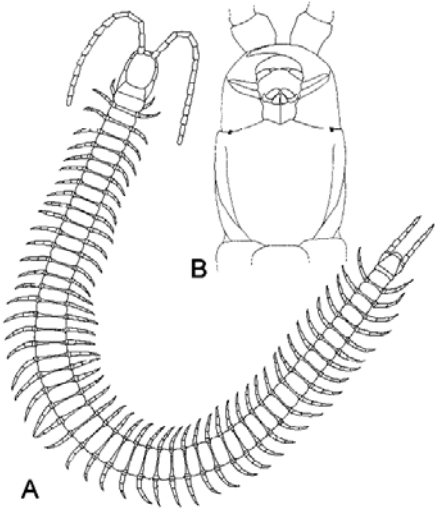

Fig. 2. Habitus of *Geophilus flavus* (Geophilomorpha: Geophilidae) (after Bonato 2011). A. whole body dorsal view. B. head, ventral view.

The family of Linotaeniidae Cook, 1899 includes ca 50 species in seven genera (Bonato 2011). These are geophilomorphs with characteristically tapering ends (fig. 3). The head is small, with slender antennae. The labrum is divided into an intermediate part often with tubercles and slightly projecting anteriorly. The mandibles have a single pectinate lamella. The forcipular segment is short and wide, with evidently tapering forcipules and tarsungulum usually furnished of a large basal tooth. Sternal pores are usually present on the posterior part of each metasternite, all along the trunk. Coxal organs open through distinct pores on the ventral surface of the coxopleura. The ultimate legs are shorter than the penultimate ones. Female gonopods are an undivided lamina. Linotaaeniids are mainly distributed in the Boreal hemisphere (North America southwards to Mexico, and temperate Eurasia).

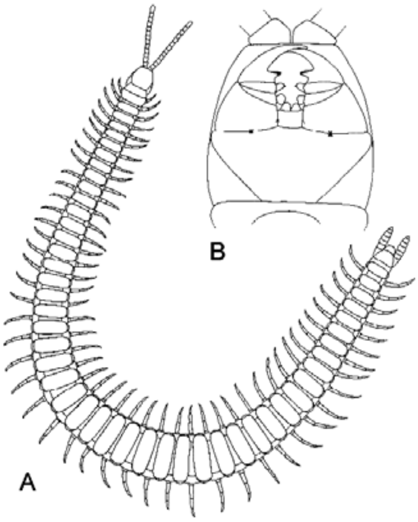

Fig. 3. Habitus of *Strigamia crassipes* (Geophilomorpha: Linotaeniidae) (after Bonato 2011). A. whole body dorsal view. B. head, ventral view

In this paper, I study the phylogeny of Geophilidae s.l., sensu Attems, documenting the diversity of morphological characters.

Materials and methods

Sampling

A total of 40 species of geophilomorphs were included in this study. External morphology was examined in mature specimens of both sexes. The specimens belong mostly to the Minelli-Bonato collection, Dipartimento di Biologia, Università di Padova but also from museum and private zoological collections and from targeted collection in the field.

Ingroup species included specimens representative of all major, morphologically distinct current genera recognizable within the Geophilidae and Linotaeniidae, except for taxa too incompletely described in literature and for which no specimens were available. For the Geophilidae the specimens analyzed belong to the following genera: *Geophilus* Leach, 1814, *Acanthogeophilus* Minelli, 1982, *Alloschizotaenia* Brölemann, 1909, *Arctogeophilus* Attems, 1909, *Arenophilus* Chamberlin, 1912, *Clinopodes* Koch, 1847, *Dinogeophilus* Silvestri, 1909, *Eurygeophilus* Verhoeff, 1899, *Geoperingueyia* Attems, 1926, *Gnathoribautia* Brölemann, 1909, *Hyphydrophilus* Pereira, Minelli & Barbieri, 1994, *Pachymerium* C.L. Koch, 1847, *Plateurytion* Attems, 1909, *Pleurogeophilus* Verhoeff, 1901, *Polycricus* Saussure & Humbert, 1872, *Polygonarea* Attems, 1909, *Ribautia* Brölemann, 1909, *Schendyloides* Attems, 1897, *Sogona* Chamberlin, 1912, *Steneurytion* Attems, 1909, *Stenotaenia* C.L. Koch, 1847, *Tuoba* Chamberlin, 1920, *Zelanophilus* Chamberlin, 1920; the genera considered for Linotaenidaee were *Strigamia* Gray, 1843 and *Tomotaenia* Cook, 1895 (tab 1).

Multiple out-groups were chosen based on the phylogenetic relationships most generally accepted for the Geophilomorpha (Foddai 1998, Foddai & Minelli 2000, Murienne et al. 2010). One species from each of the following genera was selected: *Dicellophilus* Cook 1896, (Mecistocephalidae, Placodesmata), *Schendyla* Bergsøe & Meinert, 1866, *Stigmatogaster* Latzel, 1880, *Ityphilus* Cook, 1899, *Henia* Koch, 1847, *Neogeophilus* Silvestri, 1918 (respectively Schendylidae, Himantariidae, Ballophilidae, Dignathodontidae and Neogeophilidae, all belonging to the Adesmata).

The specimens examined are listed below. They belong to the following collections: A. Minelli & L. Bonato's collection, Dipartimento di Biologia, Università di Padova (MB); Muséum National d'Histoire Naturelle, Paris (MNHNP); University of Alaska, Museum of the North, Fairbanks (UAM).

Dicellophilus carniolensis (C.L.Koch, 1874) (Mecistocephalidae): 23 specimens. Italy: Cansiglio, 20 May 2009 (L. Bonato): 1 female and 1 male (MB); Italy: Cansiglio, 8 June 1977 (A. Minelli): 1 female; Slovenia: 2 June 1991 (Gasparo): 1 male; Italy: Cansiglio, 21 July 1987 (A. Minelli): 1 male; Italy: Verona 20 July 1978 (Briganti, Gardini, Zoia): 1 male; Italy: Prealpi Bellunesi, 5 March 1985 (Paoletti): 1 female; Italy: Udine, 25 May 1979 (Gasparo): 2 female; Slovenia, 1 August 1992 (Gasparo): 1 female; Italy: Cansiglio, 6 August 1978, (Paoletti): 1 female; Italy, Montello, 8 April 2000 (Zanon): 1 male; Slovenia, 20 April 1992 (Gasparo): 1 male; Italy: Roana (VI), 30 May 1975 (Vittorelli): 1 male; Italy, Cansiglio 14 June 1972 (A. Minelli): 1 female; Slovenia, 19 April 92 (Gasparo): 1 female; Italy, Cansiglio 21 July 1973 (Minelli), 1 male; Croazia, 25 May 1991 (Gasparo): 1 female; Italy, Lavarone 7 July 1992 (Zanon): 1 female; Istria, 28 August 1990 (Gasparo): 3 females; Slovenia, 8 September 1991 (Gasparo): 1 female. (MB)

Neogeophilus sp. (Neogeophilidae): 1 specimen. Mexico: 1 male. (MB)

Stigmatogaster gracilis (Meinert, 1870) (Himantariidae): 23 specimens. Italy, Sardegna, 19-11-86 (Tonon): 1 female, 1 male; Italy, Sardegna, 16-5-80 (Torti): 2 female; Italy, Umbria 9-9-76 (Minelli): 1 female; Italy, Toscana 20-5-78 (Gardini, Briganti, Benedetti, Torchia, Zoia): 2 males; Italy, Sardegna 11-11-86 (Tonon): 3 females, 1 male; Italy, Puglia 10-6-79 (Gardini) 3 males; Tunisia, 13-2-84 (Omodeo): 1 female; Italy, Marche 12-12-92 (Gasparo): 2 males; Algeria 4-5-83 (Omodeo): 1 female; Italy, Sardegna 23-10-82 (Omodeo): 2 males, 1 female; Italy, Sardegna 12-2-86 (Tonon): 2 females. (MB)

Ityphilus sp. (Ballophilidae): 2 specimens. Lloa, Ecuador, 1-8-2006, (Giachino): 1 male, 1 female. (MB)

Schendyla nemorensis (C.L. Koch, 1837) (Schendylidae): 23 specimens. Italy, Sardegna, 20-3-1976 (Guspini): 1 female; Italy, Veneto 21-7-92 (Paoletti): 1 male; Italy, Sardegna 23-3-76 (Praticello): 11 males, 10 females. (MB)

Henia (Chaetechelyne) vesuviana (Newport, 1845) (Dignathodontidae): 23 specimens. Italy, Veneto, 4-4-2009 (Ruzzier): 1 female, 1 male; Italy, Liguria 28-3-78 (Gardini Zoia): 2 male, 1 female; Italy, Liguria 7-3-77 (Gardini): 1 female; Italy, Sicilia 25-10-81 (Minelli): 2 males; Italy, Sicilia 26-5-85 (Rizzerio, Zoia): 3 males; France, Nice 7-2-84 (Torti, Zoia): 2 females, Italy, Umbria 24-2-86 (Gardini, Rizzerio): 1 female; Italy, Liguria 13-10-85 (Gardini): 1 male; Italy, Sardegna 24-9-85 (Minelli) 1 female; Italy, Liguria 5-5-83 (Gardini): 2 males; Italy, Liguria 8-10-85 (Gardini, Rizzerio): 1 female; Italy, Emilia Romagna 11-4-85 (Torti, Zoia) 3 males; Italy, Sicilia 15-9-83 (Rizzerio): 1 female. (MB)

Strigamia acuminata (Leach, 1815) 23 specimens. Italy, Piemonte 5-11-82 (Zoia): 5 females, 3 males; Italy, Piemonte 23-6-82 (Torti, Zoia): 3 females, 3 males; Italy, Veneto, 2-12-78 (Omodeo): 1 male; Italy, Friuli 19-4-82 (Paoletti) 1 female; Italy, Friuli 14-10-79 (Paoletti): 1 male; Italy, Friuli 15-6-72 (Paoletti): 1 female; Italy, Veneto 12-4-81 (Paoletti) 1 male; Italy, Emilia Romagna 11-8-82 (Torti): 2 females. (MB)

Strigamia crassipes (C.L. Koch, 1835) 23 specimens. Italy, Udine 2-3-92 (Gasparo): 1 male; Croazia, 25-5-99 (Gasparo): 1 female; Italy, Cansiglio 1-9-77 (Paoletti): 2 females, 1male; Italy, Piemonte 20-7-78 (Gardini): 1 female; Italy, Veneto 1-8-81 (Minelli): 2 males, 1 female; Italy, Veneto 20-7-87 (Minelli): 1 female; Italy, Liguria 26-7-84 (Gardini Rizzerio Zoia): 1 male; Italy, Veneto 8-7-77 (Paoletti): 2 males. (MB)

Strigamia maritima (Leach, 1817). 2 specimens. Great Britain, LBv 1205: 1 female; LBv 1206: 1 male. (MB)

Tomotaenia sp. 2 specimens. China: LBv 188: 1 female; LBv 190: 1 male. (MB)

Acanthogeophilus dentifer Minelli, 1982 1 specimen. Italy, Trentino 28-7-81 (Minelli): 1 male. (MB)

Alloschizotaenia minuta (Silvestri, 1907). 4 specimens. MNHNP: 2 female, 2 male.

Arctogeophilus glacialis (Attems, 1909) 1 specimen. Alaska 21-07-2008 (Sikes): 1 male. (UAM)

Arenophilus sp. 1 specimen. Croazia, Istria 23-4-11 (Bonato): 1 female. (MB)

Clinopodes flavidus C.L.Koch, 1847. 23 specimens. Slovenia, 25-4-92, (Gasparo), 1 female; Croazia 16-3-91 (Gasparo): 1 male; Italy, Piemonte 19-4-79 (Zoia) 1 female; Italy, Puglia 10-2-90 (Perenzon): 1 female, 1 male; Italy, Friuli10-3-78 (Minelli): 1 female, 1 male; Jugoslavia 9-7-81 (Osello): 1 female; Italy, Friuli 9-6-68 (Minelli) 1 female; Itlay, Piemonte 16-5-82 (Torti): 1 female; Italy, Liguria 13-3-78 (Gardini, Zoia): 1 female; Italy, Puglia 2-2-90 (Pareizan): 1 female; Italy, Liguria 27-2-77 (Cassullo, Gardini, Zoia): 1 male; Italy, Piemonte 13-9-81 (Torti): 1 male; Italy, Sicilia 3-6-85 (Zoia): 1 female; Italy, Liguria 3-12-76 (Zoia, Cassullo): 1 male; Italy, Liguria 17-9-78 (Pegli, Gardini): 1 male; Italy, Liguria 5-11-78 (Gardini): 1 male; Italy, Piemonte 6-10-80 (Torti): 1 female; Italy, Toscana 20-5-78 (Gardini, Briganti, Zoia): 1 female, 1 male; Croazia 8-6-93 (Gasparo)1 male, 2 female. (MB)

Dinogeophilus oligopodus Pereira, 1984. 4 specimens. Argentina, 19-12-1985 (Pereira): 3 females, 1 male. (MB)

Eurygeophilus pinguis (Brölemann, 1898). 18 specimens. Inghilterra, 17-10-87 1 female, 1 male; Italy, Liguria, 13-2-84, (Zoia, Gardini, Rizzerio) 4 males, 12 females. (MB)

Geophilus alpinus Meinert, 1870. 23 specimens. Italy, Friuli 21-7-92 (Gasparo): 1 female; Italy, Friuli 17.5.91 (Gasparo): 1 male; Italy, Piemonte 22-6-85 (Torti): 2 males; Italy, Toscana 20-5-78 (Gardini, Briganti, Benedetti, Torchia, Zoia) 11 females, 7 males. (MB)

Geophilus carpophagus Leach, 1815. 23 specimens. Italy, Liguria 17-2-85 (Gardini): 1 female; Italy, Liguria 17-3-85 (Zoia): 1 male; Italy, Liguria 9-4-77 (Cassullo, Zoia): 6 males, 2 female; Italy, Liguria 16-1-77 (Cassulo): 1 female, 1 male; Italy, Liguria 25-9-76 (Gardini): 1 female; Italy, Liguria 4-2-86 (Gardini, Rizzerio): 1 female; Italy, Liguria 14-9-77 (Gardini, Parodi): 1 female; Italy, Liguria 30-6-86 (Gardini): 1 female; Italy, Liguria 4-2-86 (Gardini, Rizzerio): 1

male; Italy, Liguria 13-2-77 (Gardini, Parodi, Zoia): 1 female; Italy, Liguria 7-1-77 (Parodi): 2 female; Italy, Liguria 13-2-82 (Gardini, Rizzerio, Zoia): 1 female; Italy, Liguria 4-2-86 (Gardini, Rizzerio): 1 female; Italy, Liguria 25-09-00 (Foddai) 1 female. (MB)

Geophilus electricus (Linnaeus, 1758). 3 specimens. Italy, Lombardia 23-11-87 (Valle, Pandolfi): 2 females, 1 male. (MB)

Geophilus flavus (De Geer, 1778). 23 specimens. Italy, Veneto 11-12-80 (Paoletti): 1 female; Italy, Veneto 9-4-72 (Minelli): 1 male; Italy, Abruzzo 18-8-74 (Zanetti, Dioli): 1 female, 1 male; Italy, Lombardia 11-4-85 (Torti, Zoia): 3 females, 1 male; Italy, Veneto 12-2-80 (Paoletti): 2 females, 4 males; Italy, Sardegna 2-5-75 (Omodeo): 2 female; Italy, Veneto 11-12-80 (Paoletti): 2 females; Italy, Veneto 12-3-81 (Paoletti): 1 male, 1 female; Italy, Friuli 12.3.81 (Paoletti): 2 females, 1 male. (MB)

Geophilus osquidatum Brölemann, 1909. 23 specimens. Inghiterra 26-10-1988: 1 female, 1 male; France, Alpes maritimes 20-8-83 (Torti, Zoia): 2 females, 2 males; Italy, Sardegna 29-4-75 (Torti): 5 females, 4 males; Italy, Liguria 19-2-78 (Gardini, Zoia): 5 females, 3 males. (MB)

Geophilus richardi Brölemann, 1904. 23 specimens. Italy, Liguria 30-1-76 (Briganti): 1 female, 1 male; Italy, Liguria 23-06-80 (Briganti, Gardini): 1 male; Italy, Liguria 23-9-85 (Ruzziero, Zoia): 3 females, 1 male; Italy, Liguria 5-11-78 (Gardini): 11 females, 5 males. (MB)

Geophilus truncorum Bergsøe & Meinert, 1866. 5 specimens. Latvia 01-5-2003 (Spungis): 3 females, 4 males. (MB)

Gnathoribautia bonensis (Meinert, 1870). 15 specimens. Italy, Sicilia 29-4-82 (Gardini, Raniero): 1 female, 1 male; Italy, Sicilia 2-8-78 (Pace): 1 female; Tunisia 18-2-81 (Omodeo): 1 female; Spagna 5-10-71 (Omodeo) female; Italy, Sicilia 30-5-85 (Rizzerio, Zoia): 1 male; Algeria 22-10-89 (Omodeo): 1 male; Tunisia 21-10-84 (Omodeo): 1 male; Italy, Sicilia 29-5-85 (Zoia, Rizzerio) 2 females; Italy, Sicilia 22-3-69 (Osella) 1 male; Tunisia, 30-4-83 (Omodeo) 1 female; Algeria 26-10-84 (Omodeo): 1 male, 2 females. (MB)

Geoperingueyia conjungens Attems, 1928. 2 specimens. Central America: 1 female; 1 male. (MB)

Hyphydrophilus adisi Pereira, Minelli & Barbieri, 1994. 8 specimens. Brasile 25-8-82 (Pereira, Minelli): 2 females, 2 males; Brasile 20-4-77 (Pereira): 3 females, 1 male. (MB)

Pachymerium ferrugineum (Koch, 1835). 23 specimens. Italy, Sardegna 1-5-80 (Omodeo): 1 female; Italy, Sardegna 10-11-86 (Tonon): 1 male; Italy, Sicilia 27-10-81 (Minelli) 1 female; Italy, Veneto 4-5-80 (Minelli): 1 female; Italy, Veneto 13-6-00 (Bastianello): 1 male; Italy, Sardegna 13-09-86 (Tonon): 1 female; Italy, Sicilia 25-6-82 (Minelli) 1 female; Macedonia 19-4-82 (Etonti) 2 females; Italy, Liguria 11-4-79 (Giardini): 1 female; Marocco 9-9-70 (Nobile, Messina, Costa): 3 females; Algeria, 25-10-84 (Omodeo): 1 female; Italy, Piemonte 9-5-79 (Omodeo, Bonifori): 1 male; Marocco 15-9-82 (Omodeo): 6 females, 2 males; Italy, Veneto 18-6-80 (Paoletti): 1 female; Italy, Sicilia 27-10-81 (Minelli) 1 female. (MB)

Pleurogeophilus mediterraneus (Meinert, 1870). 23 specimens. Italy, Trentino 17-3-64 (Bianchi): 1 female; Italy, Veneto 4.8.74 (Moretto): 1 male; France, Alpes maritimes 25-4-80 (Zoia, Torchia): 3 females; Italy, Veneto 20-4-85 (Turcato): 3 female, 2 male; Italy, Veneto 12-5-80 (Omodeo): 1 male; Italy, Veneto 6-7-79 (Minelli): 1 female; Italy, Veneto 27-4-85 (Bortoletto): 3 females, 3 males; Italy, Liguria 22-2-82 (Vigna): 1 male, 1 female; Italy, Veneto 14.4.86 (paoletti): 1 female; Algeria 23-10-84 (Omodeo) 1 male. (MB)

Plateurytion tenebrosus (Meinert, 1886). 7 specimens. Argentina 10-10-08 (Pereira): 3 females, 2 male; Argentina 3-12-99 (Pereira): 1 female, 1 male. (MB)

Polycricus sp. 2 specimens. Mexico 27.9.93: 1 female, 1 male. (MB)

Polygonarea sp. 2 specimens. South Africa, 3-3-01 (Swaye): 1 female, 1 male. (MB)

Ribautia centralis (Silvestri, 1907). 17 specimens. Brazil 2-9-76 (Pereira): 5 females, 4 males; Brazil 19-8-97 (Pereira): 3 females, 5 males. (MB)

Ribautia ducalis Pereira, Minelli A. & Barbieri, 1995. 2 specimens. Brazil, Amazones 1-4-87 (Adis): 1 female, 1 male. (MB)

Schendyloides alacer (Pocock, 1891). 5 specimens. Agentina 15-12-85 (Cazzan): 1 females, 1 males; Argentina 15-12-85 (Pereira): 2 females, 1 male. (MB)

Steneurytion antipodum (Pocock, 1891). 1 specimen. New Zeland 15-01-00 (Edgecombe): 1 male.(MB)

Stenotaenia linearis (C.L. Koch, 1835). 23 specimens. Italy, Liguria, 10-8-80 (Zapparoli): 1 female; Italy, Liguria 13-3-78 (Gasparini): 1 male; Italy, Liguria 1-8-77 (Vigna): 1 female; Italy, Veneto 8-10-78 (Gioco): 1 female; Italy, Lombardia 21-4-79 (Paoletti): 1 male; Italy, Piemonte 27-10-78 (Torti) 1 male, 1 female; Italy, Veneto 21-7-79 (Gioco): 1 male; Italy, Piemonte 1-10-82 (Torti): 1 male; Italy, Piemonte 27-10-78 (Torti): 1 female, 1 male; Italy, Veneto 9-5-67 (Riggio): 1 female; Italy, Veneto 29-4-91 (Zanon): 1 female; Italy, Veneto 1-06-03 (Bonato): 1 female; Italy, Lombardia 6-5-79 (Torti) 1 male; Italy, Veneto 7-5-77(Omodeo): 1 male; Italy, Veneto 5-5-79 (Omodeo): 1 female; Italy, Piemonte 29-6-79 (Riese): 1 female; Italy, Piemonte 26-4-80 (Biondi, Moretti): 1 male, 1 female; Italy, Veneto 1-06-03 (Bonato): 1 male; Italy, Veneto 25-7-77 (Setta): 1 female; Italy, Piemonte 2-4-72 (Osella): 1 female. (MB)

Sogona sp. 2 specimens. Mexico, Oaxaca 8-8-73 (Brignoli): 1 male, 1 female. (MB)

Tuoba poseidonis (Verhoeff, 1901). 15 specimens. Malta, 12/02/1977: 5 females, 4 males; Italy, Sardegna 27-4-79 (Gardini): 1 female; Italy, Sardegna 23-5-80 (Gardini): 2 males; Italy, sardegna 10-2-84 (Cottarelli): 1 male. (MB)

Zelanophilus provocator (Pocock R.I., 1891). 1 specimen. New Zeland 8-12-98 (Edgecombe): 1 female. (MB)

Examination

Standardized direct examination of 468 adult specimens, both males and females, was performed using a biological microscope Leica DMLB equipped with a Leica DFC420 camera, and a stereomicroscope Leica MZ12.5 equipped with a Leica EC3 camera.

The specimens, preserved in ethanol 70%, were cleared in ethylene glycol.

Standard methods for clearing, temporary mounting in ethylene glycol as medium of inclusion, and dissecting the mouth parts of geophilomorphs (Foddai, Minelli & Pereira, 2002) were applied.

Quantitative measures and documentative photographs were taken on each specimen, under standard views in anatomical order along the antero-posterior axis and ventral/dorsal position: a series of photographs were taken at different local planes, subsequently assembled using the software Combine ZM® (Hadley, 2008).

Characters

Preliminary investigations were performed on large series of adult specimens belonging to the ingroup and outgroup species to properly define the characters. All characters were checked for their involvement in sexual dimorphism and interspecific variability, by using the program Statistica® (Statsoft, 1995).

The characters used in the previously published morphological phylogenies (Foddai 1998, Edgecombe et al. 1999, Giribet et al. 1999, Foddai & Minelli 2000, Edgecombe & Giribet 2002, Bonato et al. 2003, Edgecombe & Giribet 2004, Giribet & Edgecombe 2006, Murienne et al. 2010) were considered here whenever relevant to the species included in the present analysis; some characters which were nearly invariable within the taxon sampling were excluded after re-coding and addition of new characters, which showed a significant interspecific variability.

In total, 139 characters were considered, referring to morphological features of mature specimens, males and females (Appendix 1).

A Nexus matrix was edited to code characters with the program NDE® (NEXUS Data Editor). The characters were coded for all in-group and out-group species after the direct examination of representative specimens. The morphological characters considered were coded as binary characters, as far as possible. In order to limit the redundancy resulting from interdependence between characters, two or more originally defined characters were compounded into a single character whenever they were expected to be interdependent. When multi-state coding was required, the different states were treated as unordered. All characters were originally equally weighted. Unknown character states were coded as '?' and inapplicable data as '-'. They were given a code number indicating the position along the antero-posterior body axis. For the morphological terminology, I followed Bonato et al. (2010).

14 characters out of 139 total were of metric nature. To evaluate the validity of these characters, it was examined whether the interspecific variability was greater than the intraspecific one, using Kruskal-Wallis ANOVA test, a nonparametric test used in cases when the parameters of the distribution of the variable of interest in the population are unknown. The Kruskal–Wallis test by ranks is most commonly used when there is only one nominal variable and one measurement variable, and the latter does not meet the normality assumption of an ANOVA. It is the non-parametric analogue of a one-way ANOVA. For each of these quantitative characters, the results of a Kruskal–Wallis test were significant (Appendix 2): each character was different among the species considered and so was included in the data matrix for the phylogenetic analyses. For each character the mean and the standard error of the mean grouped by species were compared. Continuous characters were converted into discrete ones: through the frequency analysis, it was possible to aggregate the values measured into intervals.

Phylogenetic analysis

The morphological data were analyzed with the computer program TNT (tree analysis using new technology: Goloboff et al. 2003) to find the most parsimonious trees using a heuristic search with 1000 replicates of random addition sequence followed by TBR (tree bisection and reconnection) branch swapping.

Nodal support was calculated with a bootstrap analysis: subsequent to the application of the character weights obtained by the iterative procedure of successive weighting and search, 500 resamplings of characters were performed, with an equal probability among characters.

A Bayesian inference of phylogeny was also performed with the package MrBayes (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) that uses a simulation technique called Markov chain Monte Carlo (or MCMC) to approximate the posterior probabilities of trees.

Then analyses were run with one out-group species only (and all the out-groups were separately tested in this way).

Species	Family	Distribution
OUTGROUP		
Placodesmata		
Dicellophilus carniolensis (C.L. Koch, 1847)	Mecistocephalidae	Central Europe
Adesmata		
Neogeophilus sp.	Neogeophilidae	Northern America, Mexico
Stigmatogaster gracilis (Meinert, 1870)	Himantariidae	Middle, Southeastern, Southwestern Europe
Ityphilus sp.	Ballophilidae	Southern America
Schendyla nemorensis (C.L. Koch, 1837)	Schendylidae	Central Europe
Henia (Chaetechelyne) vesuviana (Newport, 1845)	Dignathodontidae	Central Europe
INGROUP		
Strigamia acuminata (Leach, 1815)	Linotaeniidae	Europe
Strigamia crassipes (C.L. Koch, 1835)	Linotaeniidae	Europe
Strigamia maritima (Leach, 1817)	Linotaeniidae	Northern Europe
Tomotaenia sp.	Linotaeniidae	Northern America and continental Asia
Acanthogeophilus dentifer Minelli, 1982	Geophilidae	Mediterranean region
Alloschizotaenia minuta (Silvestri, 1907)	Geophilidae	Eastern Africa
Arctogeophilus glacialis (Attems, 1909)	Geophilidae	Alaska
Arenophilus sp.	Geophilidae	Northern America
Clinopodes flavidus C.L.Koch, 1847	Geophilidae	Southeastern Europe
Dinogeophilus oligopodus Pereira, 1984	Geophilidae	Southern America
Eurygeophilus pinguis (Brölemann, 1898)	Geophilidae	West Europe
Geophilus alpinus Meinert, 1870	Geophilidae	West Paleartic
Geophilus carpophagus Leach, 1815	Geophilidae	Southwestern Europe, Northern Africa
Geophilus electricus (Linnaeus, 1758)	Geophilidae	Central and Northern Europe
Geophilus flavus (De Geer, 1778)	Geophilidae	West Paleartic
Geophilus osquidatum Brölemann, 1909	Geophilidae	Europe
Geophilus richardi Brölemann, 1904	Geophilidae	Southwestern Europe
Geophilus truncorum Bergsøe & Meinert, 1866	Geophilidae	Northern and Central Europe
Gnathoribautia bonensis (Meinert, 1870)	Geophilidae	Mediterranean region
Geoperingueyia conjungens Attems, 1928	Geophilidae	Southern Africa
Hyphydrophilus adisi Pereira, Minelli & Barbieri, 1994	Geophilidae	Southern America
Pachymerium ferrugineum (Koch, 1835)	Geophilidae	West Paleartic
Pleurogeophilus mediterraneus (Meinert, 1870)	Geophilidae	Northernwest Africa, Southern Europe
Plateurytion tenebrosus (Meinert, 1886)	Geophilidae	Southern America
Polycricus sp.	Geophilidae	Central America
Polygonarea sp.	Geophilidae	Southernmost Africa
Ribautia centralis (Silvestri, 1907)	Geophilidae	Southern America
Ribautia ducalis Pereira, Minelli A. & Barbieri, 1995	Geophilidae	Southern America
Schendyloides alacer (Pocock, 1891)	Geophilidae	Southernmost America
Steneurytion antipodum (Pocock, 1891)	Geophilidae	New Zeland, Australia
Stenotaenia linearis (C.L. Koch, 1835)	Geophilidae	Central Europe
Sogona sp.	Geophilidae	Southern America, Central America
Tuoba poseidonis (Verhoeff, 1901)	Geophilidae	Mediterranean region
Zelanophilus provocator (Pocock R.I., 1891)	Geophilidae	New Zeland, Australia

Tab. 1. Species considered in the analysis

Results

I included in the phylogenetic analysis 40 species, of which 34 species are the in-group and 6 species (*Dicellophilus carniolensis* (Koch, 1847), *Neogeophilus* sp., *Stigmatogaster gracilis* (Meinert, 1870), *Ityphilus* sp., *Schendyla nemorensis* (C.L. Koch, 1837) and *Henia (Chaetechelyne) vesuviana* (Newport, 1845)), the out-groups. The data matrix is given in table 2.

											1	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Dicellophilus carniolensis	3	1	1	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	2	1	1	1	1	0	0	0	0	1	1	1
Henia vesuviana	1	1	1	1	0	0	0	1	0	0	1	0	1	1	1	1	1	1	3	0	1	2	0	1	1	1	1	1	0	0
Ityphilus sp.	1	0	0	2	0	0	1	1	0	0	0	0	1	2	1	1	0	1	1	1	1	1	1	1	0	0	1	1	0	1
Neogeophilus primus	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	0	1
Schendyla nemorensis	1	1	1	2	1	0	0	0	0	0	0	0	0	2	0	0	0	1	1	1	1	1	1	1	0	1	0	1	1	2
Stigmatogaster gracilis	0	1	1	1	0	1	1	1	0	0	1	0	1	2	1	0	1	1	2	1	1	1	1	1	0	1	1	1	0	0
Acanthogeophilus dentifer	0	1	0	1	1	0	1	0	0	0	0	0	0	2	1	0	0	1	1	0	0	1	0	0	0	2	2	1	0	1
Alloschizotaenia minuta	2	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	1	1	0	0	1	2
Arctogeophilus glacialis	2	0	1	0	0	1	0	0	0	0	0	1	0	2	1	0	0	0	0	0	0	1	0	1	-	-	0	0	1	2
Arenophilus sp.	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0	1	2	1	1	1
Clinopodes flavidus	1	1	0	1	0	0	1	0	0	1	0	1	0	2	1	0	1	0	1	0	0	1	1	0	1	1	1	0	0	1
Dinogeophilus oligopodus	0	1	1	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	1	3	0	0	1
Eurygeophilus pinguis	2	1	1	1	0	0	0	1	0	1	0	0	1	1	0	0	1	0	0	0	1	1	0	1	1	1	0	0	0	0
Geoperingueyia conjungens	0	1	1	1	0	0	0	0	0	0	0	0	0	2	1	0	1	0	0	1	1	0	0	0	0	1	0	0	0	1
Geophilus alpinus	0	1	1	1	0	0	0	0	1	1	0	1	0	2	1	1	1	0	1	0	1	1	0	0	1	1	3	1	1	1
Geophilus carpophagus	2	1	1	1	0	0	1	0	1	1	0	0	0	2	1	1	0	1	1	0	1	1	0	1	0	1	2	1	0	1
Geophilus electricus	0	0	0	1	1	0	0	0	1	0	0	1	0	2	1	1	1	1	0	0	0	1	0	0	0	1	1	1	0	1
Geophilus flavus	2	2	1	2	1	0	0	0	1	1	0	1	0	2	1	1	0	1	1	0	1	1	0	0	1	2	2	0	1	1
Geophilus osquidatum	1	1	1	2	1	0	0	0	1	0	0	1	0	2	0	1	0	1	1	0	1	0	0	0	1	1	3	0	1	1
Geophilus richardi	0	1	0	1	0	1	1	0	1	1	0	1	0	1	0	1	1	1	1	0	1	1	0	1	1	1	3	0	1	1
Geophilus truncorum	0	1	0	1	0	1	0	0	1	1	0	1	0	1	1	1	1	1	2	0	0	1	0	1	0	1	2	1	0	1
Gnathoribautia bonensis	3	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	1	0	1	0	0	1	1	2
Hyphydrophilus adisi	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	1	0	0	1	3	1	1	2
Pachymerium ferrugineum	3	2	1	1	1	1	1	0	0	0	0	1	0	1	0	0	0	1	1	0	1	0	1	0	0	0	0	1	1	2
Plateurytion tenebrosus	3	2	1	1	1	0	1	0	1	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	0	1	2
Pleurogeophilus mediterraneus	3	1	1	1	0	1	1	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	0	0	1	2	1	1	1
Polycricus sp.	2	1	1	0	1	1	1	0	1	1	0	1	0	1	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	2
Polygonarea sp.	3	1	1	0	1	0	1	0	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	2
Ribautia centralis	3	2	1	1	1	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	1	1	0	1	1	3	1	1	2
Ribautia ducalis	3	2	1	1	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	1	0	1	1	3	1	1	2
Schendyloides alacer	3	1	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0	1	1	0	1	0	1	0	1	0	0	0	1	2
Sogona sp.	2	1	0	2	0	0	0	0	0	1	0	1	1	2	1	0	1	0	1	0	0	1	0	0	1	0	1	1	0	1
Steneurytion antipodum	3	2	1	1	1	1	1	0	0	0	0	1	0	1	0	0	0	1	1	1	1	1	0	0	0	1	0	1	1	2
Stenotaenia linearis	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	2	1	0	0	0	0	0	1	1	0	0	0
Strigamia acuminata	0	0	0	1	0	0	1	1	0	0	1	0	1	1	1	1	1	1	2	1	0	2	0	1	1	1	0	1	0	0
Strigamia crassipes	1	1	1	2	0	1	1	1	0	0	1	0	1	1	1	1	1	1	2	1	0	0	0	1	1	1	0	1	0	0
Strigamia maritima	1	1	0	1	0	0	1	1	0	0	1	0	1	2	0	1	1	1	2	1	0	2	0	1	1	1	0	1	0	1
Tomotaenia svenhedini	0	1	1	1	0	1	1	0	0	0	1	0	1	1	0	1	1	0	1	0	1	2	0	0	1	1	0	1	0	1
Tuoba poisedonis	1	1	0	2	0	0	1	0	0	1	0	1	0	1	1	0	0	0	1	0	0	1	0	0	0	1	1	0	0	1
Zelanophilus provocator	3	2	1	1	0	1	0	0	1	1	0	0	0	2	0	0	1	0	1	0	1	1	0	1	0	1	0	1	0	1

	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
Dicellophilus carniolensis	0	1	0	0	1	1	1	1	1	0	0	0	1	1	1	1	-	-	0	0	-	1	0	0	1	0	0	0	1	0
Henia vesuviana	0	0	0	0	0	1	1	0	0	0	3	1	0	0	0	0	-	-	-	-	-	-	1	0	0	0	0	0	0	1
Ityphilus sp.	0	0	0	1	0	1	0	1	0	0	3	1	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	1	0	1
Neogeophilus primus	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	0	0	0
Schendyla nemorensis	0	0	0	1	0	0	1	1	0	0	3	1	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	1	0	1
Stigmatogaster gracilis	0	1	0	0	0	1	1	2	0	1	0	0	0	0	0	0	-	-	-	-	-	-	0	0	0	1	0	1	1	1
Acanthogeophilus dentifer	0	0	0	1	0	1	0	0	0	0	2	0	1	1	0	0	1	1	0	1	3	1	0	0	0	0	0	0	0	1
Alloschizotaenia minuta	0	1	0	1	0	0	0	1	0	1	3	1	1	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	1
Arctogeophilus glacialis	0	1	0	1	1	0	1	1	1	1	1	0	1	0	0	0	1	1	0	0	-	-	0	0	1	0	1	0	0	1
Arenophilus sp.	0	0	0	1	0	1	1	1	0	1	3	1	1	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	1
Clinopodes flavidus	0	0	0	0	1	1	0	2	0	1	2	0	1	1	0	0	0	0	0	0	2	2	1	0	0	1	1	0	0	1
Dinogeophilus oligopodus	0	0	0	0	0	0	1	2	0	0	3	1	0	0	0	0	-	-	-	-	-	-	0	0	0	0	1	0	0	1
Eurygeophilus pinguis	0	0	0	0	0	1	0	0	1	0	2	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	1
Geoperingueyia conjungens	0	1	1	1	0	0	0	2	0	0	2	1	0	0	0	0	-	-	-	-	-	-	0	0	0	0	1	0	0	1
Geophilus alpinus	1	0	0	1	0	0	0	1	0	2	2	0	1	1	0	0	0	0	0	0	1	2	1	0	0	0	1	0	0	1
Geophilus carpophagus	0	0	0	1	0	1	1	2	0	0	2	1	1	1	0	0	1	0	0	0	1	2	1	0	0	1	1	0	0	1
Geophilus electricus	1	0	0	1	1	0	1	2	0	0	2	1	1	1	0	0	1	0	0	1	3	1	1	0	0	1	1	0	0	1
Geophilus flavus	0	0	0	1	1	0	1	1	0	1	2	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	1
Geophilus osquidatum	0	0	0	1	1	0	0	2	0	1	1	0	1	1	0	0	0	0	0	0	3	1	0	0	0	1	1	0	0	1
Geophilus richardi	0	0	0	1	0	1	0	2	0	0	1	1	1	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	0	1
Geophilus truncorum	1	0	0	1	0	1	0	2	0	0	1	1	1	1	0	0	1	0	0	1	1	1	0	0	0	1	1	0	0	1
Gnathoribautia bonensis	0	1	0	1	0	0	1	2	0	1	1	0	1	1	0	0	1	1	0	0	2	1	1	0	0	0	0	0	0	1
Hyphydrophilus adisi	0	1	0	1	0	0	1	1	0	1	1	0	1	1	0	0	1	0	0	1	1	2	1	0	0	1	0	0	0	1
Pachymerium ferrugineum	0	1	0	1	0	0	1	1	0	1	2	0	1	1	0	0	0	0	0	1	3	1	1	0	0	0	0	0	0	1
Plateurytion tenebrosus	1	1	0	1	0	0	1	1	0	1	2	0	1	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	0	1
Pleurogeophilus mediterraneus	0	0	0	0	0	1	0	1	0	1	2	1	1	1	0	0	1	0	0	1	2	1	0	0	0	0	0	0	0	1
Polycricus sp.	1	0	0	1	1	0	0	1	0	1	2	1	1	0	0	0	0	0	0	0	3	1	1	0	0	0	0	0	0	1
Polygonarea sp.	0	0	0	1	0	0	1	0	0	1	3	0	1	0	0	0	1	0	0	1	1	1	1	0	0	0	1	0	0	1
Ribautia centralis	0	1	0	1	0	1	1	1	0	1	1	1	1	1	0	0	0	1	0	0	1	2	1	0	0	0	0	0	0	1
Ribautia ducalis	0	1	0	1	0	1	1	1	0	1	1	0	1	1	0	0	1	0	0	0	1	2	1	0	0	1	0	0	0	1
Schendyloides alacer	0	0	0	1	0	0	1	1	0	1	3	0	1	1	0	0	1	0	0	1	1	2	1	0	0	0	1	0	0	1
Sogona sp.	0	0	0	0	1	1	1	0	0	1	0	0	1	1	0	0	1	0	0	0	2	1	0	0	0	1	0	0	0	1
Steneurytion antipodum	0	1	1	1	0	0	1	1	0	1	1	0	1	1	0	0	1	1	0	1	1	1	0	0	0	1	0	0	0	1
Stenotaenia linearis	0	0	0	0	0	1	0	1	0	0	2	0	1	1	0	0	0	0	0	0	2	2	1	0	0	1	1	0	0	1
Strigamia acuminata	0	0	0	1	0	1	0	0	1	0	0	0	1	1	0	0	1	1	0	0	1	0	1	1	1	0	0	0	0	1
Strigamia crassipes	0	0	0	1	0	1	0	0	1	0	0	0	1	1	0	0	1	1	0	0	1	0	1	1	1	0	0	0	0	1
Strigamia maritima	0	0	0	1	0	1	0	0	1	0	3	0	1	1	0	0	1	1	0	0	1	0	1	1	1	0	0	0	0	1
Tomotaenia svenhedini	0	0	0	1	0	1	0	2	0	0	3	0	1	1	0	0	1	1	0	0	1	0	0	1	1	0	0	0	0	1
Tuoba poisedonis	0	0	0	1	0	1	0	2	0	0	2	1	1	0	0	0	0	1	0	0	3	2	1	0	0	1	1	0	0	1
Zelanophilus provocator	0	0	0	0	1	1	1	2	1	0	0	0	1	1	1	1	-	-	0	0	-	0	1	0	0	0	0	0	0	0

	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89
Dicellophilus carniolensis	1	0	0	1	0	1	1	0	0	1	0	0	1	0	1	2	0	0	0	0	0	1	1	0	0	0	-	-	0	0
Henia vesuviana	0	0	0	1	0	1	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1	3	2	0	0
Ityphilus sp.	1	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	1	1	1	0	1	0	-	0	0	1	0	3	0	0
Neogeophilus primus	0	1	0	1	0	0	0	-	-	-	0	1	1	0	1	2	0	1	0	0	0	1	0	0	0	0	-	-	0	0
Schendyla nemorensis	1	0	0	1	0	1	0	1	1	1	1	0	1	0	0	0	1	1	1	0	1	0	-	0	0	1	0	3	0	0
Stigmatogaster gracilis	0	0	0	1	0	1	0	1	1	1	0	0	0	0	2	0	1	1	1	0	1	1	1	0	0	1	3	3	0	0
Acanthogeophilus dentifer	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	1	0	1	1	0	1	1	0	0	1	2	0	0	0	0
Alloschizotaenia minuta	0	1	0	0	0	0	0	1	1	1	0	1	1	1	2	1	0	1	1	0	1	0	-	1	0	0	-	-	0	0
Arctogeophilus glacialis	0	0	0	1	1	0	0	1	1	1	0	0	1	0	1	2	1	1	1	0	0	0	-	0	0	0	-	-	0	0
Arenophilus sp.	0	0	0	1	1	1	0	1	1	0	0	0	1	0	2	2	0	1	1	0	0	1	0	0	1	2	0	0	0	0
Clinopodes flavidus	0	1	0	0	1	1	1	1	1	1	0	0	1	0	1	1	0	1	1	0	1	1	1	0	1	2	0	0	0	0
Dinogeophilus oligopodus	0	0	0	0	1	1	1	0	1	1	0	0	1	0	2	0	0	1	0	0	1	1	0	0	1	2	1	3	0	0
Eurygeophilus pinguis	0	0	0	0	1	1	0	1	1	1	0	0	1	0	1	1	0	1	1	0	0	1	1	0	0	1	0	1	0	0
Geoperingueyia conjungens	0	0	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	-	0	1	2	0	0	1	1
Geophilus alpinus	0	0	0	0	0	1	0	1	1	1	0	0	1	0	2	1	0	1	0	0	1	1	1	0	1	2	0	3	0	0
Geophilus carpophagus	0	0	0	1	1	0	0	1	1	1	0	0	1	0	2	1	1	1	1	0	1	1	1	0	1	2	0	1	0	1
Geophilus electricus	0	0	0	1	1	1	0	1	1	1	0	0	1	0	2	1	0	1	1	0	1	1	1	0	1	2	0	4	1	0
Geophilus flavus	0	0	1	0	1	0	1	1	1	1	0	0	1	0	1	1	0	1	1	0	1	1	0	1	1	2	0	5	0	0
Geophilus osquidatum	0	0	0	0	1	0	0	1	1	1	0	0	1	0	2	1	0	1	1	1	1	1	1	1	1	2	0	5	1	0
Geophilus richardi	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	1	1	1	1	1	0	-	1	0	0	-	-	0	0
Geophilus truncorum	0	0	0	1	1	0	0	1	1	1	0	0	1	0	0	1	1	1	1	1	1	1	1	1	0	0	-	-	1	0
Gnathoribautia bonensis	0	0	0	0	1	0	0	1	1	1	1	0	1	0	1	1	0	1	1	0	1	0	-	0	0	0	-	-	0	0
Hyphydrophilus adisi	0	0	0	0	0	0	0	1	0	1	0	1	1	1	2	1	0	1	1	0	1	0	-	0	1	2	0	0	0	0
Pachymerium ferrugineum	0	0	0	1	1	0	0	1	1	1	0	0	1	0	2	1	0	1	1	0	1	1	1	0	1	2	0	0	1	1
Plateurytion tenebrosus	0	0	1	1	1	0	0	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	0	0	1	2	3	2	0	0
Pleurogeophilus mediterraneus	0	0	0	0	1	0	0	1	1	1	0	0	1	0	2	2	0	1	1	0	1	1	1	0	1	2	3	2	0	0
Polycricus sp.	0	0	0	1	1	0	1	1	1	1	0	1	1	1	1	1	0	1	1	0	1	1	1	1	1	2	2	2	1	1
Polygonarea sp.	0	0	0	0	1	0	1	1	1	1	0	0	0	1	2	0	0	1	1	0	1	0	-	0	1	2	2	0	1	0
Ribautia centralis	0	0	0	0	0	0	1	1	0	1	0	1	0	1	2	2	1	1	1	0	1	0	-	0	1	2	3	2	0	0
Ribautia ducalis	0	0	0	0	0	0	1	1	0	1	0	1	0	1	2	1	0	1	1	0	1	0	-	0	1	2	0	0	0	0
Schendyloides alacer	0	0	0	0	0	0	1	1	1	1	0	0	1	0	2	0	0	1	1	0	1	0	-	0	1	2	0	1	1	0
Sogona sp.	0	0	0	1	1	0	1	1	1	1	0	0	0	0	2	2	1	1	1	0	1	1	0	0	0	1	0	0	1	1
Steneurytion antipodum	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	1	0	1	1	0	1	1	0	0	0	0	-	-	0	0
Stenotaenia linearis	0	1	0	0	1	1	1	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	-	0	1	2	1	2	0	0
Strigamia acuminata	0	0	1	1	0	0	1	0	0	1	0	0	1	0	1	1	0	1	1	0	0	1	1	0	0	1	2	2	0	1
Strigamia crassipes	0	0	0	1	0	0	1	1	0	1	0	0	2	0	1	1	0	1	1	0	0	1	1	0	0	1	2	2	0	1
Strigamia maritima	0	0	1	1	0	0	1	0	0	1	0	0	1	0	1	1	0	1	1	0	0	1	1	0	0	1	2	2	0	1
Tomotaenia svenhedini	1	0	0	1	0	1	1	1	0	0	1	0	1	0	1	1	0	1	1	0	0	1	1	1	0	2	2	2	0	1
Tuoba poisedonis	0	1	1	0	0	1	1	1	1	1	0	0	2	0	1	1	0	1	1	0	1	1	1	0	1	2	0	0	0	1
Zelanophilus provocator	0	1	0	1	0	0	1	1	0	1	0	0	1	0	1	2	1	1	0	0	1	0	1	1	0	1	2	2	0	0

	90	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**	**116**	**117**	**118**	**119**
Dicellophilus carniolensis	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	1	1	1	1	0	1	0	1	1	1	0
Henia vesuviana	0	0	0	0	0	0	0	0	0	0	0	2	1	2	0	1	0	0	0	1	1	1	0	0	0	1	0	1	0	0
Ityphilus sp.	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0
Neogeophilus primus	0	1	1	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0	1	1	0	1	0	0	0	0	0	1	0	0
Schendyla nemorensis	0	0	1	0	0	0	0	0	0	0	0	1	1	2	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	1
Stigmatogaster gracilis	0	0	1	0	0	0	0	0	0	0	0	3	1	0	0	1	0	0	1	1	0	0	0	0	0	1	0	1	0	0
Acanthogeophilus dentifer	0	1	1	0	0	0	0	0	0	0	0	2	1	0	-	0	0	1	-	-	0	1	0	0	1	1	0	1	0	0
Alloschizotaenia minuta	0	0	1	0	0	0	0	0	0	0	0	1	1	2	0	1	0	0	0	1	1	0	0	0	0	1	0	1	1	1
Arctogeophilus glacialis	0	1	1	0	0	0	0	0	0	-	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	1	0
Arenophilus sp.	0	0	1	0	0	0	0	0	0	0	0	2	1	1	0	0	0	0	0	1	0	1	0	0	0	1	1	1	0	0
Clinopodes flavidus	0	1	1	0	0	0	0	0	0	0	0	2	1	2	0	1	0	0	0	1	0	0	1	0	1	0	0	1	1	0
Dinogeophilus oligopodus	0	1	1	0	0	0	0	0	0	0	0	0	1	2	0	0	1	0	0	0	1	1	0	0	0	1	0	1	1	0
Eurygeophilus pinguis	1	1	1	0	1	2	0	0	0	0	1	1	1	2	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0
Geoperingueyia conjungens	1	1	1	1	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	0
Geophilus alpinus	0	1	0	0	1	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Geophilus carpophagus	1	1	1	1	1	3	0	0	0	1	1	1	1	2	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0
Geophilus electricus	0	1	0	0	1	2	0	0	0	1	1	2	1	2	0	1	0	0	1	1	0	1	1	0	0	1	0	0	0	0
Geophilus flavus	0	0	1	0	1	0	0	0	0	1	1	1	1	2	1	0	0	0	0	1	0	1	1	1	0	1	0	1	0	0
Geophilus osquidatum	0	1	1	0	1	2	0	0	0	1	1	1	1	2	1	0	1	0	0	1	0	1	1	1	0	0	0	0	1	0
Geophilus richardi	0	1	1	0	1	0	0	0	0	1	1	0	1	2	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	0
Geophilus truncorum	0	1	1	0	1	3	0	0	0	0	1	1	1	2	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0
Gnathoribautia bonensis	0	0	1	0	0	0	0	0	0	0	0	2	1	2	1	1	1	0	1	1	1	0	1	0	0	1	0	1	1	0
Hyphydrophilus adisi	0	0	0	0	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0	1	1	0	0	0	1	0	0	1	1	0
Pachymerium ferrugineum	1	1	1	0	0	0	0	0	0	0	0	2	1	1	0	1	1	0	1	0	0	0	1	0	1	1	0	1	1	?
Plateurytion tenebrosus	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	1	0	1	0	0	0	1	0	1	1	0
Pleurogeophilus mediterraneus	0	1	1	0	0	0	0	0	0	0	0	2	1	1	0	1	1	1	-	-	-	1	1	0	1	1	0	1	1	0
Polycricus sp.	1	0	1	0	0	0	0	0	0	0	0	2	1	0	1	1	1	0	0	0	0	0	1	0	1	1	0	1	1	0
Polygonarea sp.	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	-	-	-	1	0	0	0	0	0	1	1	0
Ribautia centralis	0	1	1	0	0	0	0	0	0	0	0	2	1	1	1	1	1	0	0	1	0	0	1	0	1	0	0	1	1	0
Ribautia ducalis	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	1	0	1	1	0	1	0	0	1	1	0
Schendyloides alacer	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0
Sogona sp.	1	0	1	1	0	0	0	0	0	0	0	1	1	2	1	1	0	0	0	0	0	0	0	1	1	1	0	1	1	0
Steneurytion antipodum	0	1	1	0	0	0	0	0	0	0	0	1	1	2	1	0	1	0	0	1	0	1	0	0	0	0	0	1	0	0
Stenotaenia linearis	0	0	1	0	0	0	0	0	0	0	0	2	1	2	0	1	0	0	0	1	0	0	1	1	0	1	1	1	0	0
Strigamia acuminata	1	0	0	0	0	0	1	0	1	0	0	1	1	1	0	1	0	0	0	0	1	1	0	1	0	1	0	1	0	0
Strigamia crassipes	1	0	0	0	0	0	1	1	0	0	0	1	1	2	0	1	0	0	0	0	1	1	0	1	0	1	0	1	0	0
Strigamia maritima	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	1	1	0	1	0	1	0	1	0	0
Tomotaenia svenhedini	1	0	1	0	0	0	1	1	0	0	0	1	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Tuoba poisedonis	1	1	1	1	1	1	0	0	0	0	0	1	1	1	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0
Zelanophilus provocator	0	1	0	0	1	0	0	0	0	0	0	2	1	0	-	1	1	0	1	1	1	0	1	0	1	1	0	1	1	0

	120	**121**	**122**	**123**	**124**	**125**	**126**	**127**	**128**	**129**	**130**	**131**	**132**	**133**	**134**	**135**	**136**	**137**	**138**
Dicellophilus carniolensis	0	0	0	1	1	1	1	0	2	1	1	1	1	0	1	0	2	1	0
Henia vesuviana	0	1	2	1	2	0	1	1	0	1	1	1	0	0	0	0	0	1	0
Ityphilus sp.	0	1	0	0	0	0	0	0	0	1	1	2	0	0	1	0	1	0	1
Neogeophilus primus	0	0	0	0	0	0	1	0	2	1	1	0	?	?	2	?	2	1	0
Schendyla nemorensis	1	1	0	0	0	0	0	0	2	1	1	1	0	0	0	0	1	1	0
Stigmatogaster gracilis	1	1	1	0	0	0	0	0	1	1	0	-	0	0	0	0	2	1	0
Acanthogeophilus dentifer	0	0	0	0	2	1	1	0	2	1	0	-	0	1	2	0	1	0	1
Alloschizotaenia minuta	1	1	2	0	1	1	0	1	2	0	0	-	1	0	3	0	0	0	0
Arctogeophilus glacialis	1	0	0	0	0	1	1	0	1	1	1	0	0	1	0	0	0	1	1
Arenophilus sp.	0	1	0	0	0	1	?	0	2	1	0	-	0	1	0	1	2	1	0
Clinopodes flavidus	0	1	2	0	0	1	1	0	2	0	0	-	0	0	0	1	0	1	0
Dinogeophilus oligopodus	0	1	0	0	0	1	1	1	1	1	0	-	0	1	1	0	0	1	1
Eurygeophilus pinguis	0	0	0	1	2	1	1	0	0	0	0	-	0	0	0	0	0	0	0
Geoperingueyia conjungens	0	0	0	0	2	0	1	1	0	0	1	0	0	0	0	1	0	1	0
Geophilus alpinus	1	1	0	1	2	0	0	0	2	0	0	-	0	0	0	0	0	1	0
Geophilus carpophagus	1	1	0	0	2	0	1	0	1	0	0	-	1	0	0	0	0	1	0
Geophilus electricus	1	1	0	1	2	0	1	0	1	1	0	-	0	0	1	0	0	1	0
Geophilus flavus	1	1	0	0	2	0	0	0	2	0	0	-	0	0	1	0	0	1	0
Geophilus osquidatum	1	1	0	0	2	0	0	0	2	0	0	-	0	0	0	0	0	1	0
Geophilus richardi	1	1	0	0	2	0	0	0	0	1	1	0	0	0	2	0	0	0	1
Geophilus truncorum	1	1	0	0	2	0	0	0	1	1	1	0	0	0	2	0	0	0	1
Gnathoribautia bonensis	1	0	0	0	0	0	0	0	2	1	1	0	0	1	2	0	0	1	0
Hyphydrophilus adisi	1	1	0	0	2	0	1	1	2	0	0	-	1	0	3	0	0	1	0
Pachymerium ferrugineum	0	0	0	0	2	1	1	0	2	1	1	1	0	0	0	1	0	0	1
Plateurytion tenebrosus	0	1	0	0	2	1	1	0	2	0	1	0	0	1	1	1	0	0	1
Pleurogeophilus mediterraneus	0	0	0	1	0	0	1	0	2	0	0	-	0	0	1	0	0	1	0
Polycricus sp.	1	0	0	0	0	0	1	0	2	1	1	1	0	0	0	1	0	1	0
Polygonarea sp.	1	1	1	0	1	0	0	0	0	0	0	-	0	1	0	1	0	0	1
Ribautia centralis	1	1	2	0	2	1	0	1	2	0	1	1	0	1	0	0	0	1	0
Ribautia ducalis	1	1	2	0	1	1	0	1	2	0	1	0	0	1	2	0	0	1	0
Schendyloides alacer	1	1	0	0	1	0	1	0	2	1	0	-	0	0	0	1	0	1	0
Sogona sp.	1	1	0	0	2	1	1	0	0	1	0	-	0	0	0	0	0	1	1
Steneurytion antipodum	1	0	0	1	0	0	0	0	1	0	1	2	0	1	2	1	0	0	1
Stenotaenia linearis	0	1	2	0	2	0	1	0	1	0	0	-	0	0	0	1	0	1	0
Strigamia acuminata	0	0	0	0	2	0	1	0	0	0	0	-	0	0	0	0	0	1	0
Strigamia crassipes	0	0	0	0	2	0	1	0	0	0	0	-	0	0	0	0	0	1	0
Strigamia maritima	0	0	0	0	2	0	1	0	0	0	0	-	0	0	0	0	0	1	0
Tomotaenia svenhedini	0	1	0	1	2	1	1	0	0	0	0	-	0	0	0	0	0	1	0
Tuoba poisedonis	0	1	1	0	2	1	0	0	1	1	1	0	0	1	2	0	0	0	1
Zelanophilus provocator	1	0	0	1	2	1	1	0	2	1	1	0	0	1	0	0	2	1	0

Tab. 2. Data matrix with species in rows and morphological characters in columns. Symbols “-“ and “?” are used when a character doesn’t apply and where data are not avaible, respectively. (Characters describes in Appendix 1)

Morphology-based phylogenetic analysis under TNT (tree analysis using new technology; Goloboff et al. 2003)

The analysis of the data set of 139 characters (tab. 1), with *Dicellophilus carniolensis* (Koch, 1847) used to root the trees, produced 2 equally most parsimonious trees of 861 steps. (Fig. 4). After a bootstrap analysis, by means of 500 repetitions, performed in order to evaluate the phylogenetic inference, branches were maintained only where their bootstrap index was higher than 50%.

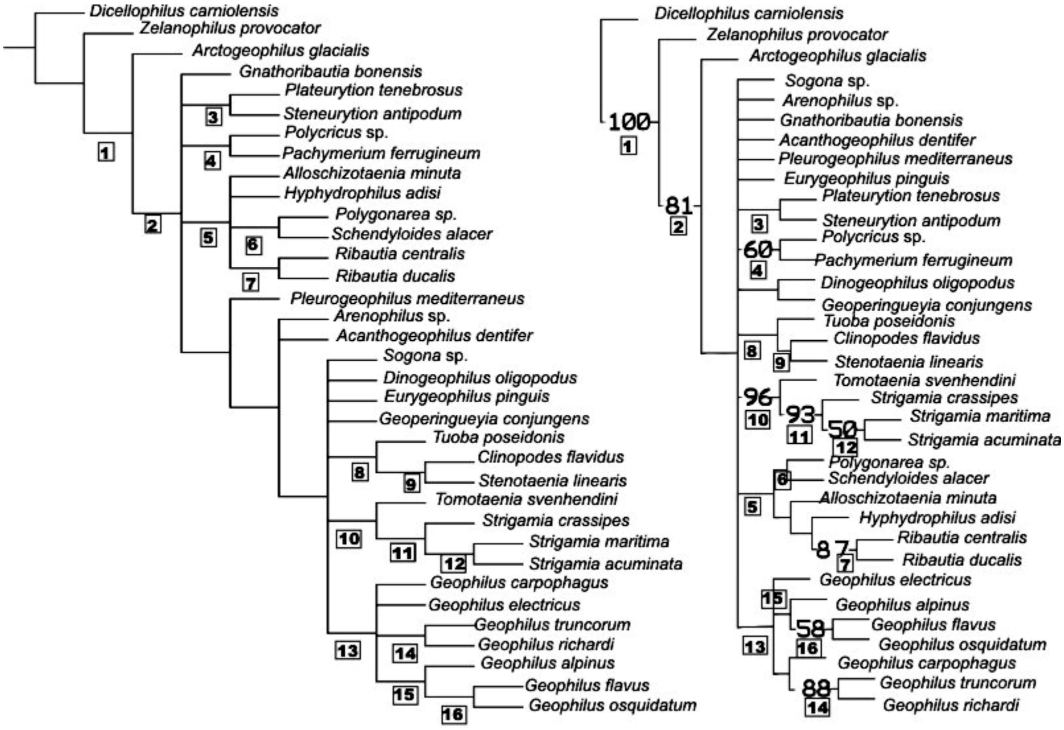

Fig. 4. Strict consensus of the most parsimonious trees for the morphological dataset under equal weighting. On the right, consensus tree with bootstrap values indicated on nodes and numbers below branches are numbered nodes repeating in all the analyses.

The parsimony analysis using *Dicellophilus carniolensis* as outgroup yielded a phylogenetic hypothesis that confirm that Geophilidae is a paraphyletic group, if Linotaeniidae is not included.

Some clades agree with traditional systematic arrangements: Geophilinae (including the current genera *Geophilus*, *Pleurogeophilus*, *Clinopodes*, *Eurygeophilus*, *Geoperyngueya*, *Dinogeophilus* and *Arenophilus*), Pachymeriinae (genera *Pachymerium* and *Eurytion*) and Chilenophilinae (genera *Ribautia*, *Arctogeophilus*, *Polygonarea*, *Gnathoribautia*, *Alloschizotaenia*) that are the subfamilies described by Attems (1929); the clade *Stenotaenia linearis*+*Clinopodes flavidus*+*Tuoba poseidonis* including in the ancient genus *Clinopodes*; *Geophilus truncorum*+*Geophilus richardi* constituting a cluster, belonged to the genus *Brachygeophilus* Brolemann 1909.

Linotaeniidae come out as a monophyletic group in which *Strigamia crassipes* and *Strigamia maritima* constitute a clade.

The geophilid *Zelanophilus provocator* has an unexpected basal position.

Characters that supported the clades are reported in fig.5 on the consensus tree.

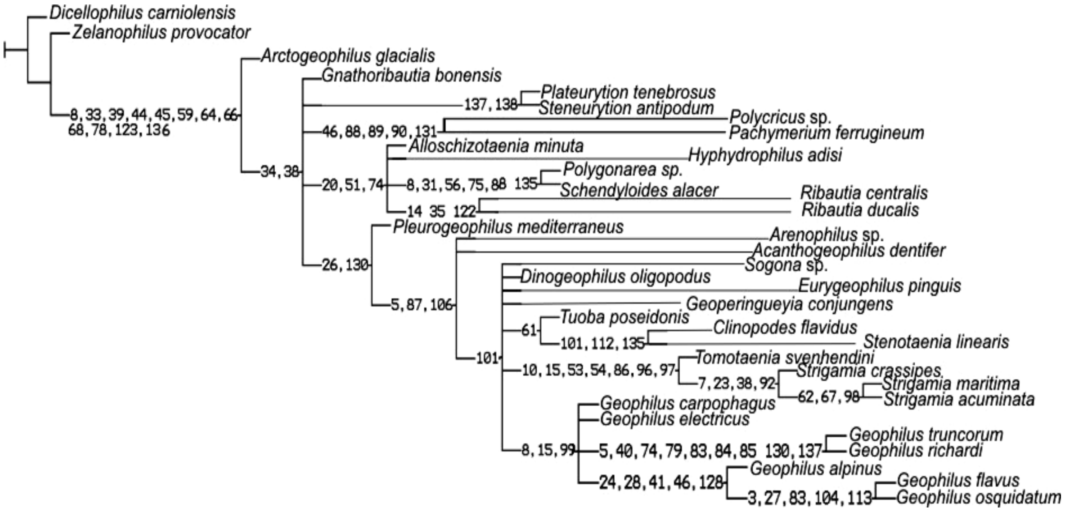

Fig. 5 Characters that supported the clades major monophyletic group, on the consensus tree. Number refer to the characters in Appendix 1.

The basal position of *Zelanophilus provocator* (node 1, fig.4) is supported by 12 synapomorphies with reversal: areolation of the cephalic plate uniform (8:0), basal denticle on the tarsungulum of the forcipular segment (33:1), clypeal area on the clypeus with setae (39:1), labrum not composed by alae (44:0), median tooth of the labrum absent (45:0), coxosternite of the first maxillae undivided mid-longitudinally (59:1), presence of coxosternal and telopodital lappet (64:1 and 68:1), dorsal hyaline scale on the coxal projection of the maxillae I (66:1), apical tubercle or claw of the maxillae II without spines (78:1), coxae of the ultimate leg-bearing segment without macropore (123:0), female gonopods fused and not articulated (136:0).

The position of *Arctogeophilus glacialis* (node 2, fig.4) is supported by 2 synapomorphies with reversal: smooth concavity of the tarsungulum of the forcipular segment (34:0), clypeus without plagulae (38:0).

The clade *Plateurytion tenebrosus*+*Steneurytion antipodum* is supported by 2 synapomorphies not unique: terminal part of the body without anal valves (137:0) and without anal organs (138:0).

The clade *Pachymerium ferrugineum*+*Polycricus* sp. (node 4, fig. 4), is supported by 5 synapomorphies: anterior margin of the median sclerite of the labrum continuous with the clypeus (46:0), pore field on the anterior part of metasternite (88:1), pores on the procoxa (89:1) and on the metacoxa (90:1), posterior part of the pregenital sternite not concave (131:1).

The clade *Alloschizotaenia minuta*+*Hyphydrophilus adisi*+*Polygonarea* sp.+*Schendyloides alacer*+*Ribautia centralis*+*Ribautia ducalis* (node 5, fig. 4) is supported by 3 synapomorphies: forcipular coxosternite not sclerotized in midline (20:0), filaments not uniform on the side-pieces of the labrum (51:1), few setae on the anterior margin of the coxosternite of the II maxillae (74:2), that is a synapomorphy with reversal for *Polygonarea* sp.

The monophyly of the clade *Polygonarea* sp.+*Schendyloides alacer* (node 6, fig. 4) is supported by 6 characters: areolation not uniform of the cephalic plate (8:1), that is a synapomorphy; forcipular trochateroprefemur without distal denticle (31:0), that is a reversal; 3 synapomorphies not unique: telopodite of the II maxillae without setae (75:0), pore field on the anterior part of metasternite (88:1), gonopods with setae (135:0).

The clade *Ribautia centralis*+*Ribautia ducalis* (node 7, fig. 4) is supported by 3 characters, one of which is a not unique synapomorphy (ratio between the maximum width of the forcipular tergite and maximum width of the first tergite is more than 0.9 – character 14:1), and 2 reversal (character 35:1 - ratio between the maximum width of the forcipular tarsungulum and the maximum length of the I article of forcipulae is more than one; character 122:2 - coxal pores of the ultimate leg-bearing segment open into pits adjacent the metasternite).

The clade *Tuoba poseidonis*+*Clinopodes flavidus*+*Stenotaenia linearis* is supported by one not unique synapomorphy: coxosternite of the first maxillae with mid-longitudinal sulcus (character 61:0).

The node 9 (*C. flavidus*+*S. linearis*) is supported by 3 reversal: number of the leg-bearing segment between 62-85 (101:2), ratio between the maximum length to the maximum width of the metasternite of the last leg bearing segment is more than one (112:1), gonopods with setae (135:0).

The clade of Linotaeniidae is supported by 3 synapomorphies: forcipular tergite subrectangular (10:1), setae scattered on the forcipular tergite (15:1), labrum are divided into superior and inferior lamellae, with teeth on superior lamella directed anteriorly (character 53:1); it is also supported by 2 reversal (stilus on the cephalic pleurite - 54:1 - and more than one pore fields on the posterior part of the sternite - 86:2) and by 2 synapomorphies with reversal (transverse suture on the sternite - 96:1 - and longitudinal suture on the sternite - 97:1).

The node 11 (fig. 4) is supported by 4 characters: 2 synapomorphies (lateral margin of the cephalic plate rounded and not parallel - 7:1 - and procoxa and metacoxa not divided by a sulcus - 92:0) and 2 reversal (lateral margin of the forcipular coxosternite not parallel - 23:1 - plagulae on the clypeus – 38:1).

The clade *Stigamia acuminata+Strigamia maritima* is supported by 2 synapomorphies: median longitudinal cleft on the anterior border of the coxosternite of the I maxillae (62:1), shallow circular depression on the sternite of leg-bearing segment (98:1); it is also supported by one reversal: telopodite of the I maxillae constituted by one article (67:0).

The clade of Geophilus is supported by 3 characters: 1 reversal (areolation not uniform of the cephalic plate, 8:1) and 2 synapomorphies (setae not scattered on the forcipular tergite, 15:1, 3 longitudinal gutter well marked on the sternite, 99:1).

The monophyly of the clade *Geophilus truncorum+Geophilus richardi* is supported by 4 not unique synapomorphies: coxosternite of the II maxillae without setae (74:0), metatergites subtrapezoidal (79:1), metasternites subtrapezoidal (83:1), terminal part of the body without anal valves (137:0); it is also supported by 5 reversal: transverse suture on the cephalic plate (5:1), setae of the clypeus few in number patterned in a pair of postantennary setae, a pair of intermediate setae and a pair of posterior setae (40:1), transition on the leg-bearing segment (84:0), sternites without ventral pores (85:0), pregenital sternite on the terminal part of the body (130:1).

The clade *Geophilus alpinus+Geophilus flavus+Geophilus osquidatum* is supported by 1 not unique synapomorphy (character 24:1, coxopleural sutures only ventral) and by 4 reversal: ratio of maximum length to maximum width of the I article of the forcipulae more than 1.2 (28:1), complete suture between clypeus and labrum (41:0), anterior margin of mid-piece not continuous with the clypeus (46:1), ratio of maximum length of last leg to maximum length of penultimate leg more than 1,4 (128:2).

The clade *Geophilus flavus+Geophilus osquidatum* is supported by 5 characters: the degree of elongation of the XIV article of the antennae is between 2,5 and 3,5 (3:2), forcipular coxosternite without setae (27:0), pretergite of the ultimate leg-bearing segment with setae not uniform distributed (104:1), metasternite of the ultimate leg-bearing segment (113:1); it is also supported by 1 probable reversal: pore fields on the anterior part of the metasternite of the leg-bearing segment (88:1).

All other out-groups belonging to the Adesmata were separately tested.

The analysis with *Neogeophilus* sp. as outgroup produced 15 equally most parsimonious trees of 835 steps. A bootstrap analysis was performed in the same modality of the preceding bootstrap test (fig. 6).

As phylogenies based on morphological and molecular data agree in grouping together Himantariidae, Ballophilidae and Schendylidae that are a clade only distantly related with Geophilidae s.l. sensu Attems, I tested one species of each families as outgroup.

Using *Stigmatogaster gracilis* as outgroup, 8 equally most parsimonious trees of 864 steps were obtained (fig. 7). 7 most-parsimonious tree (868 steps) were produced with *Ityphilus* sp. as outgroup and 4 with *Schendyla nemorensis* (836 steps). (figs. 8 and 9 respectively).

The analysis of the data set including *Henia vesuviana* (Dignathodontidae) as outgroup yielded 2 most-parsimonious trees of 832 steps (fig. 10).

All the analyses with different outgroups confirmed the monophyly of the same clades obtained with *Dicellophilus carniolensis* as outgroup.

The characters that supported each node in the different analyses are almost the same (tab. 3).

The position of the geophilid *Zelanophilus provocator* changes in the different analyses: it has a well- supported basal position with *Dicellophilus carniolensis* and *Neogeophilus* sp. as outgroup; probably this specie deserves to be included in a distinct (still unnamed) family.

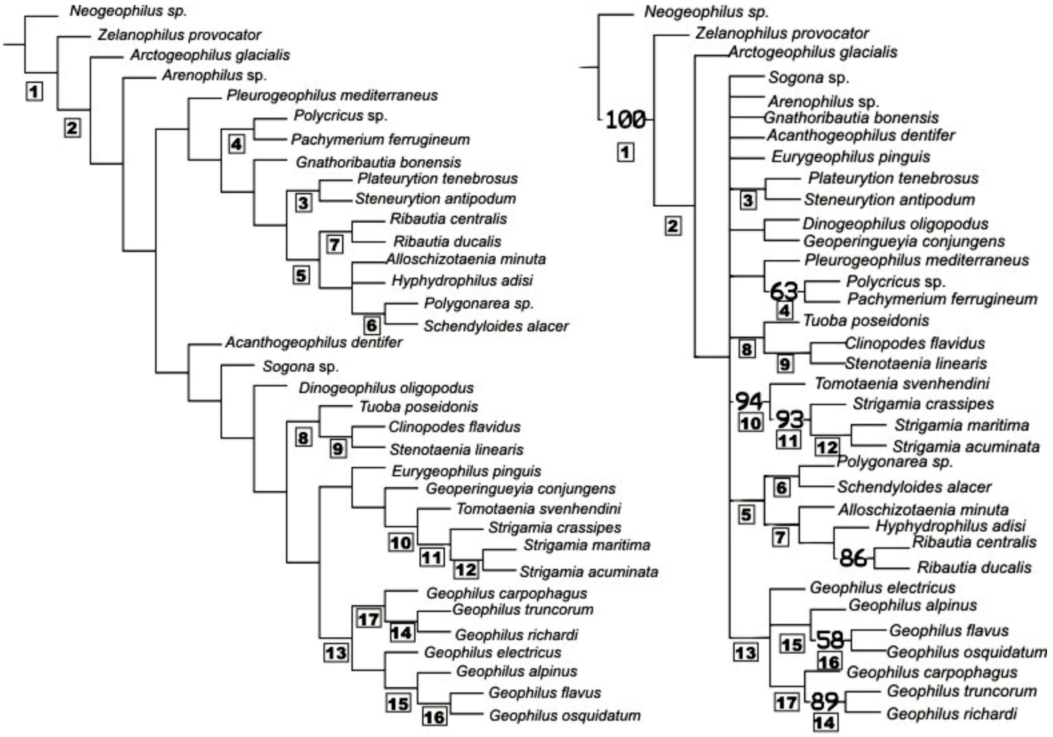

Fig. 6. Strict consensus of the most parsimonious trees for the morphological dataset with *Neogeophilus* sp. as outgroup. On the right, consensus tree with bootstrap values indicated on nodes and numbers below branches are the nodes recovered in all the analyses.

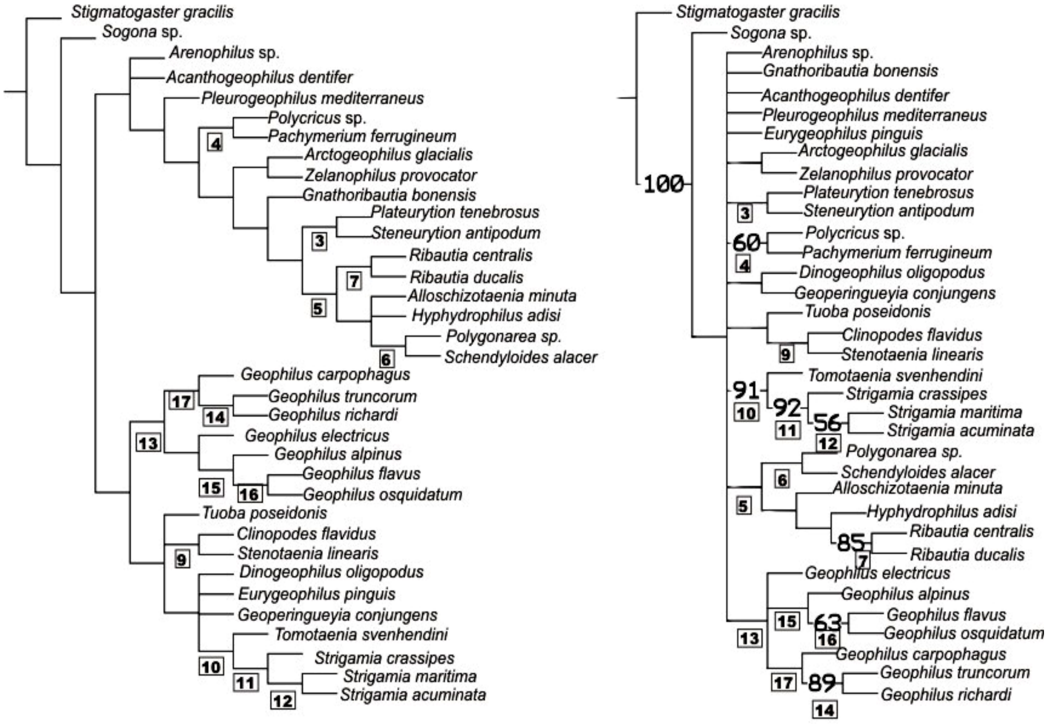

Fig. 7. Strict consensus of the most parsimonious trees for the morphological dataset with *Stigmatogaster gracilis* as outgroup. On the right, consensus tree with bootstrap values indicated on nodes and numbers below branches are the nodes recovered in all the analyses.

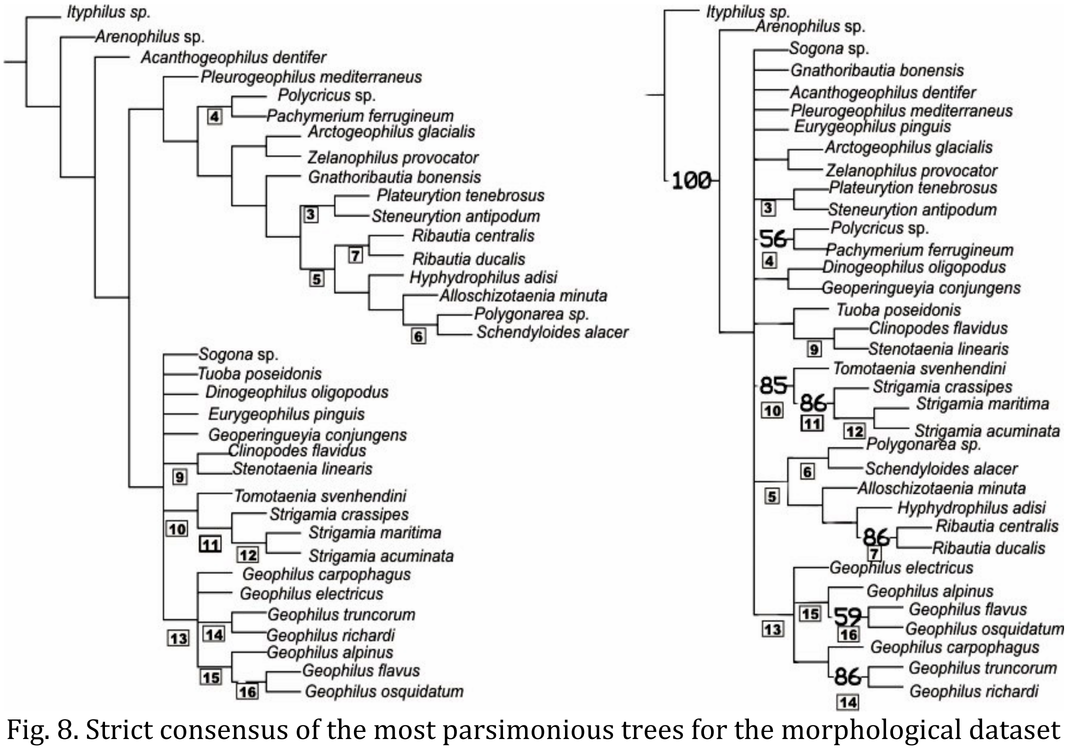

Fig. 8. Strict consensus of the most parsimonious trees for the morphological dataset with *Ityphilus* sp. as outgroup. On the right, consensus tree with bootstrap values indicated on nodes and numbers below branches are the nodes recovered in all the analyses.

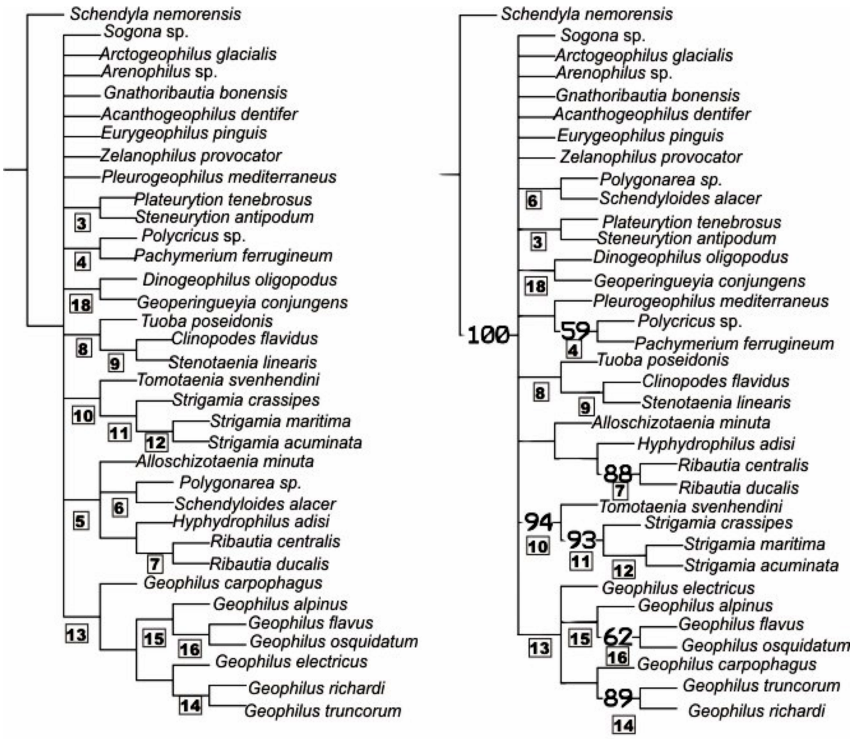

Fig. 9. Strict consensus of the most parsimonious trees for the morphological dataset with *Schendyla nemorensis* as outgroup. On the right, consensus tree with bootstrap values indicated on nodes and numbers below branches are the nodes recovered in all the analyses.

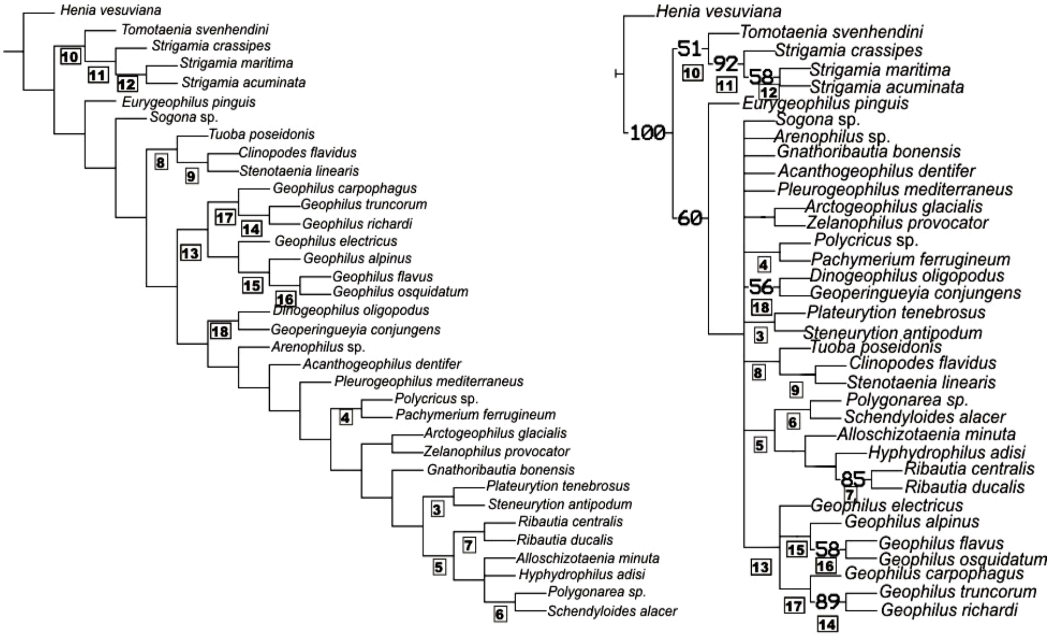

Fig. 10. Strict consensus of the most parsimonious trees for the morphological dataset with *Henia vesuviana* as outgroup. On the right, consensus tree with bootstrap values indicated on nodes and numbers below branches are the nodes recovered in all the analyses.

node	**outgroup** *Dicellophilus carniolensis*	**outgroup** *Neogeophilus* **sp.**	**outgroup** *Stigmatogaster gracilis*	**outgroup** *Ityphilus* **sp.**	**outgroup** *Schendyla nemorensis*	**outgroup** *Henia vesuviana*
1	8,33,39,44,45,59,64,66,68,78,123,136	8,11,28,33,39,59,61,64,78,106				
2	34,38	26,34,74,84,85,108,130				
3	137,138	52,11,135,137,138	6,52,81,111,135,137,138	6,52,81,111,135,	1,55,72,137,138	6,52,81,111,135,137,138
4	46,88,89,90,131	46,50,88,89,90,131,135	25,46,50,88,89,90,109,131,135	25,46,88,89,90,131,135	25,46,88,89,90	25,46,50,88,89,90,109,131,135
5	20,51,74	20,51	20,51,74	20,51,74,127	124,130.	20,51,74
6	8,31,56,75,88,135	8,31,56,71,75,88,135	8,31,56,71,75,88,135	8,31,56,66,71,75,88,103,127,134,1	8,56,88,135	8,31,56,71,75,88,89,90,109,131,135
7	14,35,122	14,35,122,125	14,35,122	14,35,66,103,122	1,14,35,72,91,104,106,112,130	14,35,122
8	61	6,46,51,61,105			61	6,27,46,51,61,63
9	101,112,135	41,101,111,112,135	101,111,112,135	112,135	102,112,135	41,101,111,112,129,135
10	10,15,53,54,86,96,97	6,10,15,27,41,53,54,56,63,66,86,91,96,97,105	10,15,27,41,43,53,54,56,63,86,91,96,97	10,15,53,54,86,87,96,97	6,9,10,15,21,53,54,96,97	6,33,41,53,54,89,96,97
11	7,23,88,92	7,17,20,23,37,38,85,92,109,113,117	17,92,109,113,117	7,17,23,38,92	7,17,18,19,125	18,19,20,38,65,109,113,121,123
12	62,67,98	2,62,67,98	2,62,67,98	62,67,98	2,62,67,98	2,62,67,98
13	8,15,99	8,15,17,27,99,120	8,15,99,100	8,15,99	8,15,99,120	8,15,17,50,94,99,100,120,125
14	5,40,74,79,83,84,85,130,137	5,40,49,74,79,83,84,85,126,130,134,137,138	5,13,40,49,74,79,83,84,85,126,130,134,137,138	5,13,40,74,79,83,84,85,130,137	5,13,40,74,76,79,83,84,85,130,137,138	5,40,49,74,79,83,84,85,126,130,134,137,138
15	24,28,41,46,128	24,26,28,41,46,126,128	24,26,28,46,63,126,128	24,28,41,128	24,28,41,46,63,128	2,24,28,41,46,63,126,128,129
16	3,27,83,104,113	3,16,27,65,83,104,113	3,16,27,83,104,113	3,27,83,104,113	3,4,27,34,83,104,113	3,16,27,65,83,104,113

Characters are indicated by their respective code numbers as in appendix I

Tab. 3. Characters supporting each node in the analyses with different outgroup.

Morphology-based phylogenetic analysis under MrBayes

The same analyses performed under TNT were repeated with MrBayes using the Bayesian inference.

Figure 11 shows the analysis performed with *Dicellophilus carniolensis* as out-group. Then, all the other outgroups were separately tested (figs. 12-13-14-15-16).

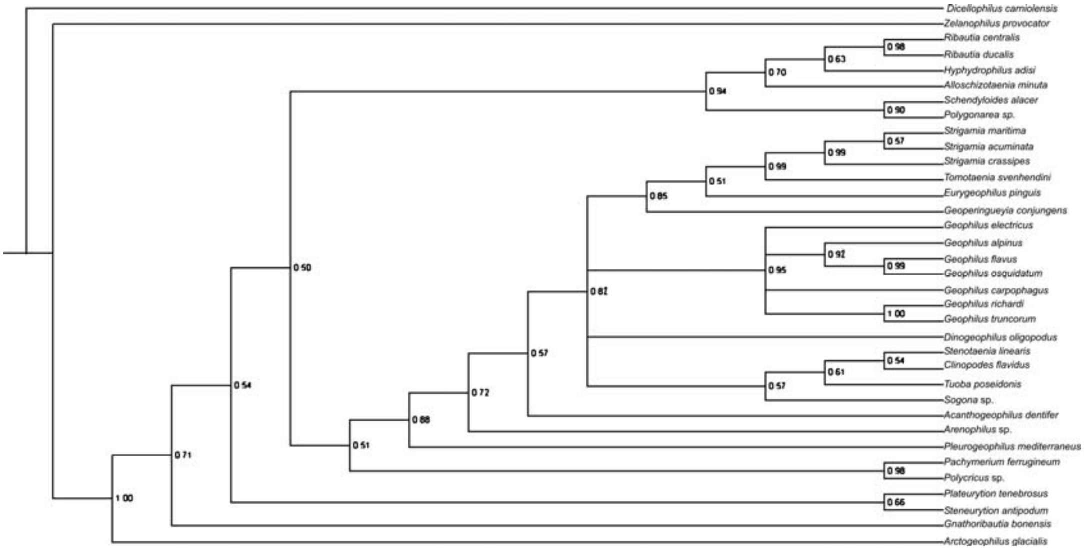

Fig. 11. Phylogeny obtained by Bayesian inference with *Dicellophilus carniolensis* as out-group. The number at the node indicated the clade credibility that gives the probability of each partition or clade in the tree.

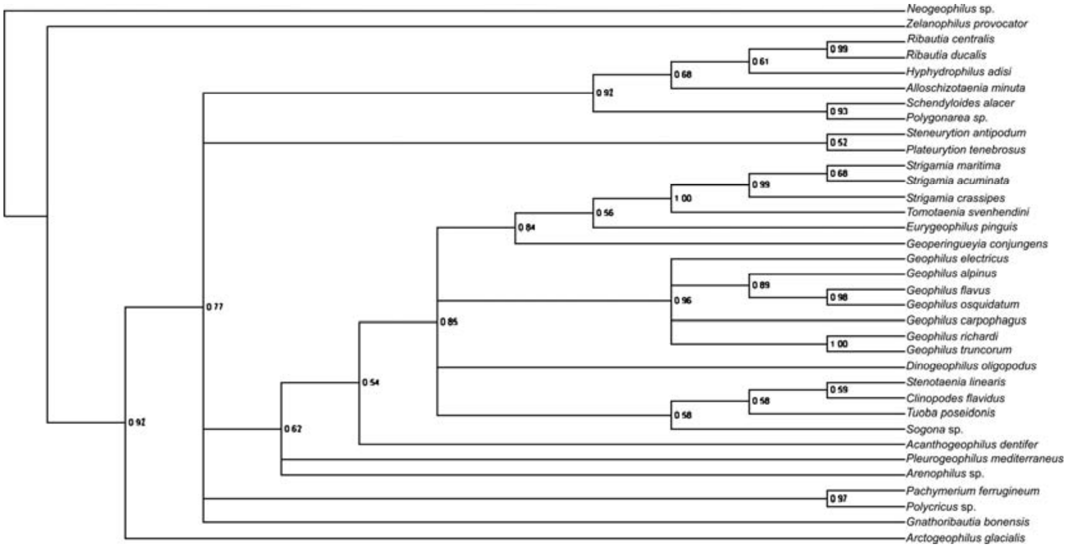

Fig. 12. Phylogeny obtained by Bayesian inference with *Neogeophilus* sp. as out-group. The number at the node indicated the clade credibility that gives the probability of each partition or clade in the tree.

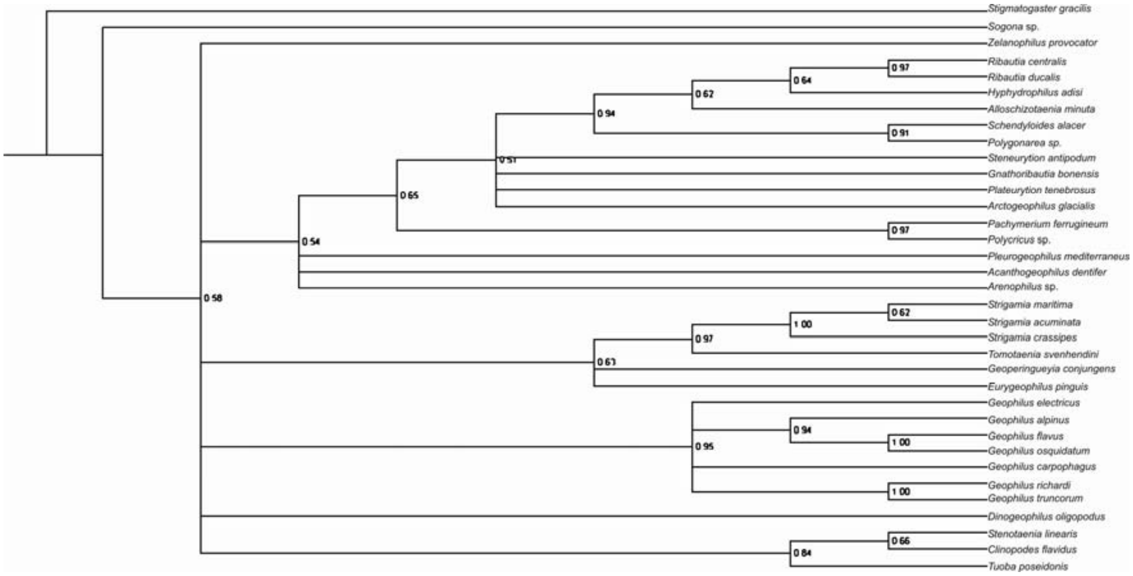

Fig. 13. Phylogeny obtained by Bayesian inference with *Stigmatogaster gracilis* as out-group. The number at the node indicated the clade credibility that gives the probability of each partition or clade in the tree.

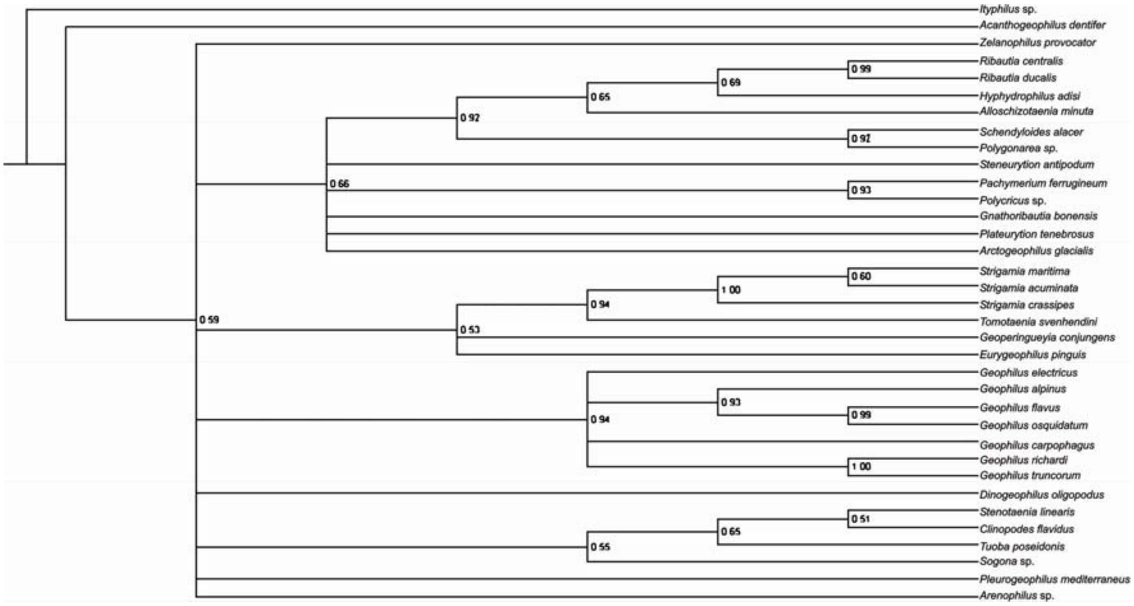

Fig. 14. Phylogeny obtained by Bayesian inference with *Ithyphilus* sp. as out-group. The number at the node indicated the clade credibility that gives the probability of each partition or clade in the tree.

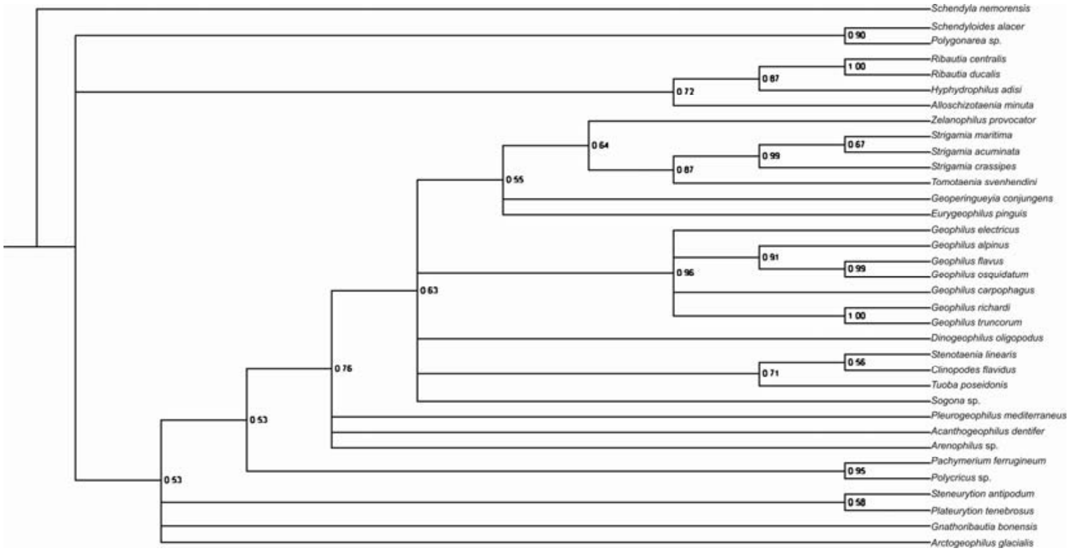

Fig.15. Phylogeny obtained by Bayesian inference with *Schendyla nemorensis* as out-group. The number at the node indicated the clade credibility that gives the probability of each partition or clade in the tree.

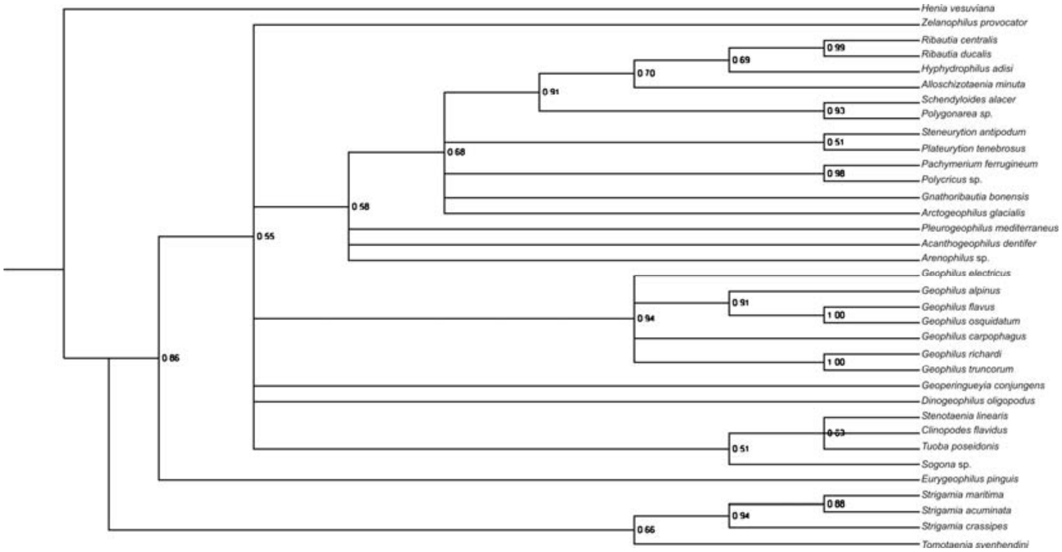

Fig. 16. Phylogeny obtained by Bayesian inference with *Henia vesuviana* as out-group. The number at the node indicated the clade credibility that gives the probability of each partition or clade in the tree.

The analyses performed with the Bayesian inference, using different outgroups, confirmed the results obtained with TNT. In all trees, the clades *Steneurytion antipodum+Plateurytion tenebrosus, Pachymerium ferrugineum+ Polycricus* sp., *Ribautia centralis+Ribautia ducalis+Hyphydrophilus adisi +Alloschizotaenia minuta+Schendyloides alacer+Polygonarea* sp., *Schendyloides alacer +Polygonarea* sp., *Ribautia centralis+Ribautia ducalis, Tuoba poseidonis*

+*Clinopodes flavidus*+*Stenotaenia linearis*, *Clinopodes flavidus*+*Stenotaenia linearis*, Linotaeniidae, genus *Strigamia*, *Strigamia maritima*+*Strigamia acuminata*, genus *Geophilus*, *Geophilus truncorum*+*Geophilus richardi*, *Geophilus alpinus*+*Geophilus flavus*+*Geophilus osquidatum*, *G. flavus*+*G.osquidatum* are supported as in the phylogenies under TNT.

Discussion

The phylogenetic relationships among chilopod orders and families have been previously investigated both with molecular and morphological data (Edgecombe et al. 1999, Giribet et al. 1999, Foddai and Minelli 2000, Edgecombe and Giribet 2002, 2004, Giribet and Edgecombe 2006, Murienne et al. 2010). All the analyses recognized a basal split between Mecistocephalidae and all other geophilomorphs (Adesmata), as proposed by Verhoeff (1908 in Verhoeff 1902-1925). Maternal brooding behaviour (Bonato and Minelli 2002) as well as molecular analyses (Edgecombe et al. 1999, Edgecombe and Giribet 2004) identified plesiomorphic character states in Placodesmata (Mecistocephalidae) relative to Adesmata. This basal division is also retrieved in the morphological cladistic analysis of Foddai and Minelli (2000), the only work that included exemplars of all families of Geophilomorpha, and provided the current phylogenetic framework.

The current analysis is more exhaustive for Geophilidae s.l than any previously published phylogeny with respect to the number of genera taken into account: Foddai and Minelli considered only 5 genera of Geophilidae and 1 genus of Linotaeniidae, here I considered 23 genera of Geophilidae and 2 genera of Linotaeniidae. The parsimony and Bayesian analyses recognized Geophlidae s.l. as a paraphyletic group: the Geophilidae (a part from *Zelanophilus provocator*) is united in a clade with Linotaeniidae, as found by recent molecular data (Murienne et al. 2010).

The geophilid *Zelanophilus provocator* has an unexpected basal position in the order: contrary to the current inclusion in the family of Geophilidae, this species could be included in a new family, because of its different characters respect to the other geophilids (e.g. labrum composed by alae and median tooth) and its distribution are restricted to the New Zealand.

Within the Geophilidae sl. several monophyletic clades can be recognized. One of these corresponds to the Linotaeniidae; a second clade is constituted by the genus *Geophilus*. The monophyly of a group including *Tuoba posedonis*, *Clinopodes flavidus* and *Stenotaenia linearis* is congruent with the old concept of the genus *Clinopodes* C.L. Koch, 1847 that included all these taxa (Bonato et al. 2011). The clade *Polygonarea* sp., *Schendyloides alacer*, *Alloschizotaenia minuta*, *Hyphydrophilus adisi* and *Ribautia* belonged to Attems's subfamily Chilenophilinae. The monophyly of *Polycricus* sp.+*Pachymerium ferrugineum* is congruent with Attems (1903) and Brolemann (1930) who considered *Polycricus* sp. as a synonym of *Pachymerium* C.L. Koch, 1847. Concerning the other species included in this analysis, the phylogeny is not resolved confidently.

Probably an exhaustively sampled molecular survey is the next step in retrieving a better phylogeny that also can serve as a basis for geophilds taxonomy.

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Appendix 1: characters used in the phylogenetic analysis

0. **Antennae, basal distance (mm):**
    0. <0,02
    1. ≥0,02; <0,04
    2. ≥0,04; <0,08
    3. ≥0,08
1. **Antennae, VII article, maximum length/maximum width:**
    0. ≥0,4; <1
    1. ≥1; <1,6
    2. ≥1,6
2. **Antennae, XIV article, maximum length/maximum width:**
    0. <2
    1. ≥2
3. **Antennae maximum length/cephalic plate maximum length:**
    0. <2,5
    1. ≥2,5; <3,5
    2. ≥3,5
4. **Cephalic plate, maximum length/maximum width:**
    0. <1,2
    1. ≥1,2
5. **Cephalic plate, transverse suture:**
    on the anterior part of the dorsal side of the cephalic capsule (Bonato et al. 2010)
    0. absent
    1. present
6. **Cephalic plate, cephalic sutures:**
    a pair of shallow groves, longitudinally on the posterior part of cephalic plate (Bonato et al. 2010)
    0. absent
    1. present
7. **Cephalic plate, lateral margins, shape:**
    0. straight, parallel
    1. rounded, not parallel
8. **Cephalic plate, areolation:**
    0. uniform
    1. not uniform
9. **Forcipular pretergite:**
    short sclerite anterior to the forcipular tergite (Bonato et al. 2010)
    0. not visible
    1. present
10. **Forcipular tergite, shape:**
    main tergite of the forcipular segment (Bonato et al. 2010)
    0. subtrapezoidal
    1. subrectangular
11. **Forcipular tergite, medial length/ maximum width:**

    0. <0,4
    1. ≥0,4
12. **Forcipular tergite, lateral margins:**
    0. convergent anteriorly, straight
    1. convex sides
13. **Forcipular tergite, posterior end:**
    0. narrower than head
    1. as broad as head
    2. broader than head
14. **Forcipular tergite maximum width/T1 maximum width:**
    0. <0,9
    1. ≥0,9
15. **Forcipular tergite, setae:**
    0. scattered
    1. not scattered
16. **Forcipulae and forcipular pleurites:**
    0. exposed dorsally
    1. overlapped by the head and forcipular tergites when viewed dorsally
17. **Forcipular segment, poison calyx, shape:**
    0. cylindrical
    1. not cylindrical
18. **Forcipular segment, poison calyx, position:**
    0. within the tarsungulum
    1. in other articles
    2. in the trochanteroprefemur
    3. in the trunk
19. **Forcipular segment, cerrus:**
    short setae on the dorsal surface of the forcipular coxosternite (Bonato et al. 2010)
    0. absent
    1. present
20. **Forcipular coxosternite sclerotized in midline:**
    0. no
    1. yes
21. **Forcipular coxosternite, anterior margin:**
    0. almost straight
    1. with a shallow concavity
    2. with a broad, deep concavity
22. **Forcipular coxosternite, coxosternal denticles:**
    small subconical projection on the anterior margin of the forcipular coxo-sternite (Bonato et al. 2010)
    0. absent
    1. present
23. **Forcipular coxosternite, lateral margin:**
    0. almost parallel in the anterior part
    1. not parallel

24. **Forcipular coxosternite, coxopleural sutures:**
suture between the forcipular pleurite and the forcipular coxosternite (Bonato et al. 2010)
    0. anterior part dorsal, posterior part ventral
    1. ventral only
25. **Forcipular coxosternite, coxopleural sutures:**
    0. running parallel to the lateral margin of pleurite for most of its length
    1. convergent posteriorly, rounded
    2. not extending to the anterolateral angle of the forcipular coxosternite but terminating laterally
26. **Forcipular coxosternite, chitin lines:**
paramedian sclerotised narrow stripes on the ventral side of the forcipular coxosternite (Bonato et al. 2010)
    0. absent
    1. present, complete
    2. present, incomplete distally, pointing to the condyles
    3. present, incomplete distally, divergent from the condyles
27. **Forcipular coxosternite, setae:**
    0. absent
    1. present
28. **Forcipular segment, I article of the forcipulae, maximum length/maximum width:**
    0. <1,20
    1. ≥1,20
29. **Forcipular segment, I article of the forcipulae, maximum length/ coxosternum maximum width:**
    0. ≥0,2; <0,3
    1. ≥0,3; <0,5
    2. ≥0,5
30. **Forcipular trochanteroprefemur, proximal denticle:**
the most basal of two denticles along the mesal side of the forcipular trochanteroprefemur (Bonato et al. 2010)
    0. absent
    1. present
31. **Forcipular trochanteroprefemur, distal denticle:**
the most distal of two denticles along the mesal side of the forcipular trochanteroprefemur (Bonato et al. 2010)
    0. absent
    1. present
32. **Forcipular segment, II and III articles of the forcipulae, sclerotized teeth on the internal side:**
    0. absent
    1. present
33. **Forcipular segment, tarsungulum, basal denticle:**
at the base of the forcipular tarsungulum (Bonato et al. 2010)
    0. absent

    1. present

34. **Forcipular segment, tarsungulum, concavity:**
    0. smooth
    1. crenulate

35. **Forcipular segment, tarsungulum maximum width/I article maximum length:**
    0. ≥0,5; <1
    1. ≥1

36. **Forcipular segment, bulge on articles:**
    0. absent
    1. present

37. **Clypeus, paraclypeal sutures:**
    lateral margins of the clypeus (Bonato et al. 2010)
    0. absent, not visible
    1. present, parallel
    2. present, not parallel

38. **Clypeus, plagulae:**
    non-areolate areas on the posterior part of the clypeus (Bonato et al. 2010)
    0. absent
    1. present

39. **Clypeus, clypeal area:**
    small, subcircular, finelly areolate area on the areolate part of the clypeus (Bonato et al. 2010)
    0. absent
    1. present, with setae
    2. present, without setae

40. **Clypeus, setae:**
    0. numerous, scattered and not patterned
    1. few in number, patterned in a pair of postantennary setae, a pair of intermediate setae and a pair of posterior setae
    2. few in number, with setae also outsides the symmetrical pattern of postantennary, intermediate and posterior setae
    3. few in number, not patterned

41. **Clypeolabral suture:**
    suture between clypeus and labrum (Bonato et al. 2010)
    0. complete, distinct
    1. incomplete

42. **Labrum, concave arc:**
    0. yes
    1. no

43. **Labrum, sclerite:**
    0. one
    1. more than one

44. **Labrum, anterior and posterior alae and transverse thickened line:**
    ala: one of the two sclerites composing the labral side-piece

transverse thickened line: sclerotized ridge between the anterior and the posterior ala of the labral side-piece (Bonato et al. 2010)

0. absent
1. present

45. **Labrum, median tooth:**

0. absent
1. present

46. **Labrum, mid-piece or intermediate part, anterior margin:**

median sclerite of the labrum (Bonato et al. 2010)

0. continuous with the clypeus
1. anterior suture complete

47. **Labrum, mid-piece or intermediate part, posterior margin:**

0. straight
1. not straight

48. **Labrum, side-pieces or lateral parts, anterior margin:**

0. complete
1. continuous with clypeus

49. **Labrum, side-pieces or lateral parts, posterior margin, shape:**

0. rounded
1. almost straight

50. **Labrum, mid-piece or intermediate part:**

filament: hair-like, sometimes branching, projection along the posterior mar-gin of the labrum;

teeth: subconical, stout projection along the posterior margin of the labrum (Bonato et al. 2010)

0. without distinct teeth or filaments
1. bearing teeth
2. fringed with filaments
3. bearing teeth and filaments

51. **Labrum, side-pieces or lateral parts, filaments:**

0. absent
1. present, length not uniform
2. present, length uniform

52. **Labral tubercles:**

subconical, stout projection along the posterior margin of the labrum (Bonato et al. 2010)

0. absent
1. present

53. **Labrum divided into superior and inferior lamellae, with teeth on superior lamella directed anteriorly:**

0. absent
1. present

54. **Cephalic pleurite, stilus:**

sclerotised ridge on the mesal margin of the cephalic pleurite (Bonato et al. 2010)

0. absent
1. present

55. **Cephalic pleurite, setae:**
    0. absent
    1. present
56. **Cephalic pleurite, mesal notch:**
    0. absent
    1. present
57. **Mandible, dentate lamella:**
    tooth-like, one ore none on each mandible (Bonato et al. 2010)
    0. absent
    1. present
58. **Mandible, pectinate lamella, numbers:**
    comb-like, one to several on each mandible (Bonato et al. 2010)
    0. single
    1. multiple
59. **Maxillae I, coxosternite:**
    0. divided mid-longitudinally
    1. undivided mid-longitudinally
60. **Maxillae I, coxosternite, areolation:**
    0. uniform
    1. not uniform
61. **Maxillae I, coxosternite, mid-longitudinal sulcus:**
    0. absent
    1. present
62. **Maxillae I, coxosternite, anterior border, median longitudinal cleft:**
    0. absent
    1. present
63. **Maxillae I, coxosternite, setae:**
    presence of one or few setae on the antero-internal corner of each of the two halves of the first maxillary coxosternum (Bonato et al. 2010)
    0. absent
    1. present
64. **Maxillae I, coxosternal lappet:**
    lappet on the first maxillary coxosternite (Bonato et al. 2010)
    0. absent
    1. present
65. **Maxillae I, coxal projection, distal part, shape:**
    paired projections on the anterior margin of the first maxillary coxosternite, mesal to the telopodites (Bonato et al. 2010)
    0. subtriangular
    1. not subtriangular
66. **Maxillae I, coxal projections, dorsal hyaline scales:**
    hyaline scales arranged in a narrow band, longitudinally aligned on the dorsal surface and close to the internal margin of the projection (Bonato et al. 2010)
    0. absent
    1. present

67. **Maxillae I, telopodite, articles, numbers:**
telopodites: paired projections articolated on the anterior margin of the first maxillary coxosternite, lateral to the coxal projections (Bonato et al. 2010)
    0. 1
    1. 2
68. **Maxillae I, telopodital lappet:**
lappet on the basal article of the first maxillary telopodite (Bonato et al. 2010)
    0. absent
    1. present
69. **Maxilla I, telopodite, setae:**
    0. absent
    1. present
70. **Maxillae II, areolation:**
    0. uniform
    1. not uniform
71. **Maxillae II, coxosternite:**
    0. undivided
    1. divided mid-longitudinally
72. **Maxillae II, coxosternite, anterior margin:**
    0. partially divided by a median cleft
    1. broadly concave with no trace of median notch
    2. shallow concave
73. **Maxillae II, coxosternite, isthmus:**
isthmus: median part of the secon maxillary coxosternite (Bonato et al. 2010)
    0. sclerotized, continuous with the lateral parts
    1. hyaline, different from the lateral parts
74. **Maxilla II, coxosternite, setae:**
    0. absent
    1. present, many scattered
    2. present, few, along the anterior margin
75. **Maxillae II, telopodite, setae:**
    0. absent
    1. present, few in number
    2. present, many
76. **Maxillae II, III article, setae, distribution:**
third article of the second maxillary telopodite (Bonato et al. 2010)
    0. lacking from the most basal part of the article
    1. scattered over the whole surface
77. **Maxillae II, pretarsus:**
terminal element articulated to the most distal article of the second maxillary telopodite (Bonato et al. 2010)
    0. apical tubercle
    1. apical claw
78. **Maxillae II, apical tubercle or claw:**

0. with small spines
1. without spines

79. **Leg-bearing segment, metatergites, shape:**
posterior sclerite of the two dorsal sclerites of a leg-bearing segment (Bonato et al. 2010)
0. subrectangular
1. subtrapezoidal

80. **Leg-bearing segment, tergites, paramedian sulci:**
paired paramedian longitudinal sulci on a tergite (Bonato et al. 2010)
0. absent
1. present

81. **Leg-bearing segment, presternite:**
anterior region of the single sternite of a leg-bearing segment (Bonato et al. 2010)
0. absent
1. present

82. **Leg-bearing segment, presternite:**
0. not coxtricted medially
1. costricted medially

83. **Leg-bearing segment, metasternites, shape:**
posterior region of the single sternite of a leg-bearing segment (Bonato et al. 2010)
0. subrectangular
1. subtrapezoidal

84. **Leg-bearing segment, transition:**
loss of sternal pattern, division of the pore group, termination of carpophagus structure
0. absent
1. present

85. **Leg-bearing segment, ventral pores:**
glandular pores on the ventral side of leg-bearing segment (Bonato et al. 2010)
0. absent
1. present from the first to the penultimate sternite with the same pattern
2. present but without the same pattern along the trunk

86. **Leg-bearing segment before the transition, pore field:**
an area of clustered pores on the ventral side of a leg-bearing segment (Bonato et al. 2010)
0. one, transversely elongate, on the posterior part of the sternite
1. one, longitudinally elongate, on the posterior part of the sternite
2. more than one, on the posterior part of the sternite
3. one, transversely elongate, on the central part of the sternite

87. **Leg-bearing segment, pore field:**

0. in preferred but unstructured areas, narrow band
1. in preferred but unstructured areas, diffuse band
2. in well defined areas, of circular shape
3. in well defined areas, of oval or reniform shape
4. in well defined areas, of diamond shape
5. in well defined areas, of transversely triangular shape

88. **Leg-bearing segment, metasternite, pore field on the anterior part:**
    0. absent
    1. present
89. **Leg-bearing segment, procoxa, pores:**
    subcoxa anterior to the coax (Bonato et al. 2010)
    0. absent
    1. present
90. **Leg-bearing segment, metacoxa, group of pores:**
    subcoxa posterior to the coxa (Bonato et al. 2010)
    0. absent
    1. present
91. **Leg-bearing segment, procoxa and metacoxa:**
    0. same length
    1. procoxa longer than metacoxa
92. **Leg-bearing segment, sulcus between procoxa and metacoxa:**
    0. absent
    1. present
93. **Leg-bearing segment, presternites and adjacent pleurites, pore fields:**
    0. absent
    1. present
94. **Leg-bearing segment, carpophagus pegs:**
    median projection on the posterior margin of a sternite, in the carpophagus-structure (Bonato et al. 2010)
    0. absent
    1. present
95. **Leg-bearing segment, carpophagus pits:**
    median socket on the anterior margin of a sternite, in the carpophagus-structure (Bonato et al. 2010)
    0. absent
    1. present, occupying almost the whole breadth of sternite
    2. present, occupying 3/4 of the breadth of sternite
    3. present, occupying nearly half the width of sternite
96. **Leg-bearing segment, sternite transverse suture:**
    transverse suture on a sternite (Bonato et al. 2010)
    0. absent
    1. present

97. **Leg-bearing segment, sternite longitudinal suture:**
    mid-longitudinal suture on a sternite (Bonato et al. 2010)

0. absent
1. present

98. **Leg-bearing segment, shallow circular depression:**
   0. absent
   1. present

99. **Leg-bearing segment, longitudianal gutter:**
   longitudinal groove on the sternite (Bonato et al. 2010)
   0. median longitudinal gutter and feeble lateral gutter
   1. 3 longitudinal gutter well marked

100. **Leg-bearing segment, metasternites, configuration in mesosternal area, prosternal area, pores area and post sternal area:**
   each sternite anterior to the transition shows a well defined pattern of smooth areas with fainter reticulation: a large rectangular mesosternal area behind which, on either side, is a oblong poststernal area (Eason, 1964)
   0. absent
   1. present

101. **Leg-bearing segment, number:**
   0. < 35
   1. ≥35; <61
   2. ≥62; <85
   3. ≥85

102. **Leg-bearing segment, same number in all specimens in both sexes:**
   0. yes
   1. no

103. **Ultimate leg-bearing segment, ultimate pretergite:**
   pretergite of the ultimate leg-bearing segment (Bonato et al. 2010)
   0. shorter than metatergite of penultimate segment
   1. as broad as metatergite of penultimate segment
   2. longer than metatergite of penultimate segment

104. **Ultimate leg-bearing segment, pretergite, setae:**
   0. uniform distribution
   1. not uniform distribution

105. **Ultimate leg-bearing segment, pleuropretergite:**
   entire sclerite corresponding to the ultimate pretergite and the two intercalary pleurites (Bonato et al. 2010)
   0. separated from the adjacent pretergite
   1. fused to the adjacent pretergite

106. **Last leg bearing segment, metatergite maximum length/maximum width:**
   0. <1
   1. ≥1

107. **Ultimate leg-bearing segment, coxopleuron exposed dorsally:**
   0. yes
   1. no

108. **Ultimate leg-bearing segment, coxal pores on the dorsal surface:**
    0. absent
    1. present

109. **Ultimate leg-bearing segment, coxopleuron, lateral margin converging anteriorly:**
    0. yes
    1. no

110. **Ultimate leg-bearing segment, coxopleuron setae:**
    0. present, few, not uniform distribution
    1. present, uniform

111. **Ultimate leg-bearing segment, presternite:**
    0. bilobous
    1. not bilobous

112. **Last leg bearing segment, metasternite maximum length/maximum width:**
    0. <1
    1. ≥1

113. **Ultimate leg-bearing segment, metasternite:**
    0. not constricted by coxopleura
    1. constricted by coxopleura

114. **Ultimate leg-bearing segment, metasternite :**
    0. broader than long
    1. longer than broad

115. **Ultimate leg-bearing segment, metasternite, posterior border:**
    0. rounded
    1. not rounded

116. **Ultimate leg-bearing segment, metasternite:**
    main sternite of the ultimate leg-bearing segment (Bonato et al. 2010)
    0. trapeziform
    1. not trapezioform

117. **Ultimate leg-bearing segment, metasternite, setae:**
    0. uniform
    1. not uniform, setae especially concentrated on the posterior part of sternite and the internal part of coxopleura

118. **Last leg bearing segment, coxa maximum length/maximum width:**
    0. <1,8
    1. ≥1,8

119. **Ultimate leg-bearing segment, coxopleuron, bulge on the posterior-internal part:**
    0. absent
    1. present

120. **Ultimate leg-bearing segment, coxopleuron, setae:**
    0. few, uniformly distributed
    1. scattered

121. **Ultimate leg-bearing segment, coxal pores:**
    0. distributed over the entire surface of the coxa

1. concentrated along the edge of the adjacent metasternite, in two distinct rows

122. **Ultimate leg-bearing segment, coxal pores open:**
   0. directly onto surface
   1. into pits adjacent the metasternite, opening of coxal glands into one poche
   2. into pits adjacent the metasternite, opening of coxal glands into more than one pouches

123. **Ultimate leg-bearing segment, coxae, macropore:**
   coxal pore distincty larger than the other pores (Bonato et al. 2010)
   0. absent
   1. present

124. **Ultimate leg, pretarsus:**
   apical element articulated at the tip of the leg (Bonato et al. 2010)
   0. absent
   1. tubercle
   2. claw

125. **Ultimate leg, accessory spines:**
   slender, pointed projection at the base of the claw (Bonato et al. 2010)
   0. absent
   1. present

126. **Ultimate leg:**
   0. as slender in males as in females
   1. swollen in males, slender in females

127. **Ultimate leg, article numbers:**
   0. 6
   1. not 6

128. **Last leg maximum length/penultimate leg maximum length:**
   0. <1.2
   1. ≥1,2; <1,4
   2. ≥1,4

129. **Terminal part of the body, intermediate sternite:**
   sternite between the sternite of the ultimate leg bearing segment and the pregenital sternite (Bonato et al. 2010)
   0. absent
   1. present

130. **Terminal part of the body, pregenital sternite:**
   sternite between the intermediate sternite and the genital sternite, usually associated with gonopods (Bonato et al. 2010)
   0. apparently absent
   1. present

131. **Terminal part of the body, pregenital sternite, posterior margin:**
   0. concave
   1. not concave
   2. angulated

132. **Terminal part of the body, genital sternite:**
   sternite posterior to the pregenital sternite (Bonato et al. 2010)

  - 0. entire
  - 1. not entire

133. **Terminal part of the body, genital sternite setae:**
  - 0. uniformly distributed, low density
  - 1. not uniformly distributed

134. **Terminal part of the body, genital sternite, posterior margin:**
  - 0. straight
  - 1. angulated
  - 2. concave
  - 3. without margin between genital sternite and gonopodial lamina

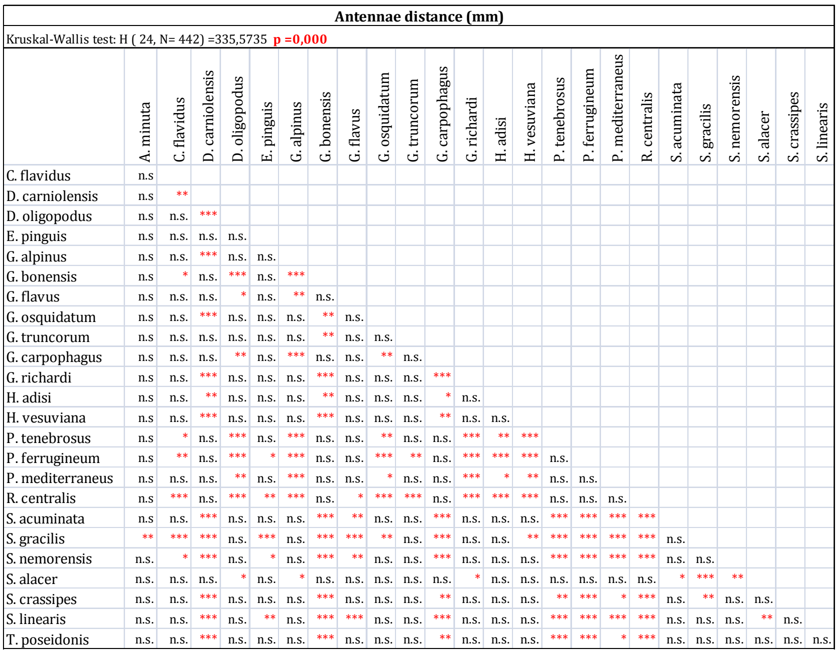
135. **Terminal part of the body, gonopods:**
  - 0. with setae
  - 1. without setae

136. **Terminal part of the body, female gonopods:**
  - 0. fused and not articulated
  - 1. distinct and uniarticulated
  - 2. distinct and biarticulated

137. **Terminal part of the body, anal valves:**
  - 0. absent
  - 1. present

138. **Terminal part of the body, anal organs:**
  - 0. present
  - 1. absent

Appendix 2: analysis of quantitative characters

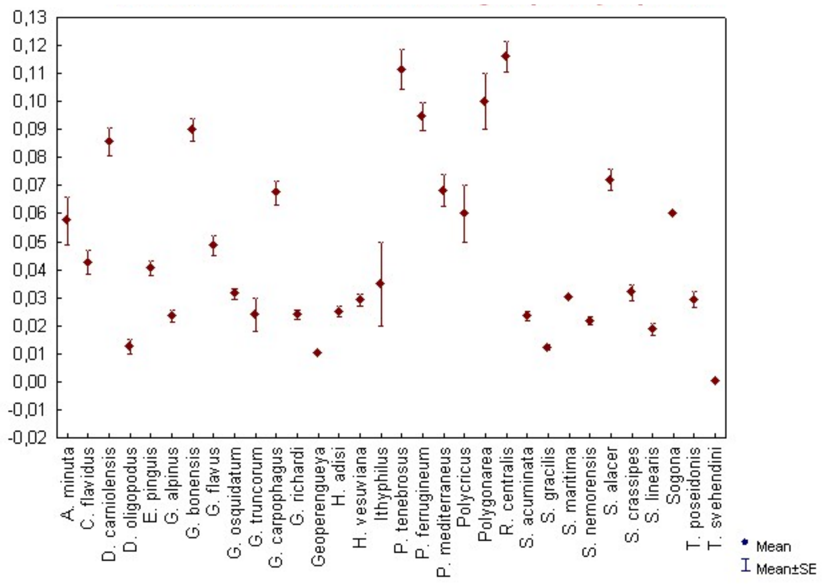


Antennae distance (mm)

Kruskal-Wallis test: H (24, N= 442) =335,5735 **p =0,000**

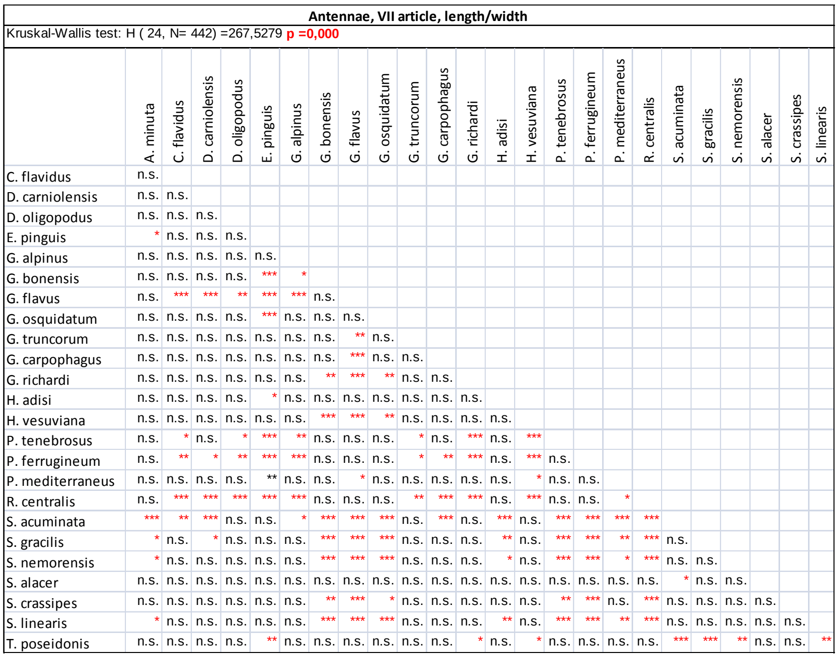
	A. minuta	C. flavidus	D. carniolensis	D. oligopodus	E. pinguis	G. alpinus	G. bonensis	G. flavus	G. osquidatum	G. truncorum	G. carpophagus	G. richardi	H. adisi	H. vesuviana	P. tenebrosus	P. ferrugineum	P. mediterraneus	R. centralis	S. acuminata	S. gracilis	S. nemorensis	S. alacer	S. crassipes	S. linearis
C. flavidus	n.s																							
D. carniolensis	n.s	**																						
D. oligopodus	n.s	n.s.	***																					
E. pinguis	n.s	n.s.	n.s.	n.s.																				
G. alpinus	n.s	n.s.	***	n.s.	n.s.																			
G. bonensis	n.s	*	n.s.	***	n.s.	***																		
G. flavus	n.s	n.s.	n.s.	*	n.s.	**	n.s.																	
G. osquidatum	n.s	n.s.	***	n.s.	n.s.	n.s.	**	n.s.																
G. truncorum	n.s	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.															
G. carpophagus	n.s	n.s.	n.s.	**	n.s.	***	n.s.	n.s.	**	n.s.														
G. richardi	n.s	n.s.	***	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	***													
H. adisi	n.s	n.s.	**	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	*	n.s.												
H. vesuviana	n.s	n.s.	***	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	**	n.s.	n.s.											
P. tenebrosus	n.s	*	n.s.	***	n.s.	***	n.s.	n.s.	**	n.s.	n.s.	***	**	***										
P. ferrugineum	n.s	**	n.s.	***	*	***	n.s.	n.s.	***	**	n.s.	***	***	***	n.s.									
P. mediterraneus	n.s	n.s.	n.s.	**	n.s.	***	n.s.	n.s.	*	n.s.	n.s.	***	*	**	n.s.	n.s.								
R. centralis	n.s	***	n.s.	***	**	***	n.s.	*	***	***	n.s.	***	***	***	n.s.	n.s.	n.s.							
S. acuminata	n.s	n.s.	***	n.s.	n.s.	n.s.	***	**	n.s.	n.s.	***	n.s.	n.s.	n.s.	***	***	***	***						
S. gracilis	**	***	***	n.s.	***	n.s.	***	***	**	n.s.	***	n.s.	n.s.	**	***	***	***	***	n.s.					
S. nemorensis	n.s.	*	***	n.s.	*	n.s.	***	**	n.s.	n.s.	***	n.s.	n.s.	n.s.	***	***	***	***	n.s.	n.s.				
S. alacer	n.s.	n.s.	n.s.	*	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	***	**			
S. crassipes	n.s.	n.s.	***	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	**	***	*	***	n.s.	**	n.s.	n.s.		
S. linearis	n.s.	n.s.	***	n.s.	**	n.s.	***	***	n.s.	n.s.	***	n.s.	n.s.	n.s.	***	***	***	***	n.s.	n.s.	n.s.	**	n.s.	
T. poseidonis	n.s.	n.s.	***	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	***	***	*	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

a.



b.

Fig. 1. A2. Analyses of the quantitative character “antennae distance in mm”: a. The results of a Kruskal–Wallis test are significant (H= 333.5735, P=0.000); the mean ranks of antennae distance in mm are significantly different among the species (*=0,5-0,1; **=0,1-0,01; ***<0,01). b. Comparison of mean and standard error of the antennal distance grouped by species.

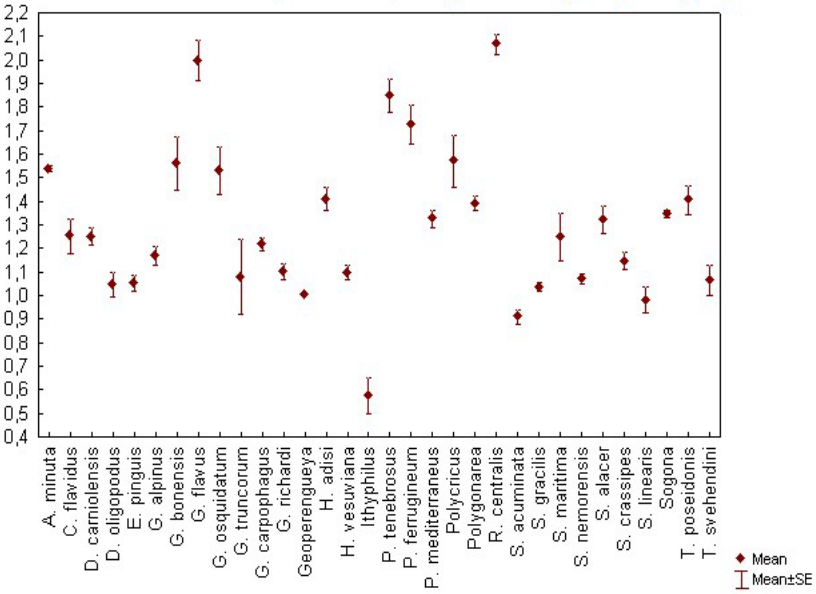


Antennae, VII article, length/width

Kruskal-Wallis test: H (24, N= 442) =267,5279 p =0,000

	A. minuta	C. flavidus	D. carniolensis	D. oligopodus	E. pinguis	G. alpinus	G. bonensis	G. flavus	G. osquidatum	G. truncorum	G. carpophagus	G. richardi	H. adisi	H. vesuviana	P. tenebrosus	P. ferrugineum	P. mediterraneus	R. centralis	S. acuminata	S. gracilis	S. nemorensis	S. alacer	S. crassipes	S. linearis
C. flavidus	n.s.																							
D. carniolensis	n.s.	n.s.																						
D. oligopodus	n.s.	n.s.	n.s.																					
E. pinguis	*	n.s.	n.s.	n.s.																				
G. alpinus	n.s.	n.s.	n.s.	n.s.	n.s.																			
G. bonensis	n.s.	n.s.	n.s.	n.s.	***	*																		
G. flavus	n.s.	***	***	**	***	***	n.s.																	
G. osquidatum	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.																
G. truncorum	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.															
G. carpophagus	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.														
G. richardi	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	***	**	n.s.	n.s.													
H. adisi	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.												
H. vesuviana	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	***	**	n.s.	n.s.	n.s.	n.s.											
P. tenebrosus	n.s.	*	n.s.	*	***	**	n.s.	n.s.	n.s.	*	n.s.	***	n.s.	***										
P. ferrugineum	n.s.	**	*	**	***	***	n.s.	n.s.	n.s.	*	**	***	n.s.	***	n.s.									
P. mediterraneus	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.								
R. centralis	n.s.	***	***	***	***	***	n.s.	n.s.	n.s.	**	***	***	n.s.	***	n.s.	n.s.	*							
S. acuminata	***	**	***	n.s.	n.s.	*	***	***	***	n.s.	***	n.s.	***	n.s.	***	***	***	***						
S. gracilis	*	n.s.	*	n.s.	n.s.	n.s.	***	***	***	n.s.	n.s.	n.s.	**	n.s.	***	***	**	***	n.s.					
S. nemorensis	*	n.s.	n.s.	n.s.	n.s.	n.s.	***	***	***	n.s.	n.s.	n.s.	*	n.s.	***	***	*	***	n.s.	n.s.				
S. alacer	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.			
S. crassipes	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	***	*	n.s.	n.s.	n.s.	n.s.	n.s.	**	***	n.s.	***	n.s.	n.s.	n.s.	n.s.		
S. linearis	*	n.s.	n.s.	n.s.	n.s.	n.s.	***	***	***	n.s.	n.s.	n.s.	**	n.s.	***	***	**	***	n.s.	n.s.	n.s.	n.s.	n.s.	
T. poseidonis	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	*	n.s.	n.s.	n.s.	n.s.	***	***	**	n.s.	n.s.	**

a.



b.

Fig. 2. A2. Analyses of the quantitative character “VII antennal article: ratio of maximum length and maximum width ”: a. The results of a Kruskal–Wallis test were significant (H= 267,5279, P=0.000); the mean ranks of the ratio of maximum length and maximum width of the VII antennal article are significantly different among the species (*=0,5-0,1; **=0,1-0,01; ***<0,01). b. Comparison of mean and standard error of the antennal distance grouped by species.

a.

Antennae, XIV article, length/width

Kruskal-Wallis test: H (24, N= 442) =142,1926 **p =,0000**

	A. minuta	C. flavidus	D. carniolensis	D. oligopodus	E. pinguis	G. alpinus	G. bonensis	G. flavus	G. osquidatum	G. truncorum	G. carpophagus	G. richardi	H. adisi	H. vesuviana	P. tenebrosus	P. ferrugineum	P. mediterraneus	R. centralis	S. acuminata	S. gracilis	S. nemorensis	S. alacer	S. crassipes	S. linearis
C. flavidus	n.s.																							
D. carniolensis	n.s.	n.s.																						
D. oligopodus	n.s.	n.s.	n.s.																					
E. pinguis	n.s.	n.s.	n.s.	n.s.																				
G. alpinus	n.s.	n.s.	n.s.	n.s.	n.s.																			
G. bonensis	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.																		
G. flavus	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.																	
G. osquidatum	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.																
G. truncorum	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.															
G. carpophagus	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.														
G. richardi	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	**	n.s.	n.s.	n.s.													
H. adisi	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.												
H. vesuviana	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.											
P. tenebrosus	n.s.	**	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	***	n.s.	n.s.										
P. ferrugineum	n.s.	***	***	n.s.	n.s.	**	n.s.	n.s.	**	***	*	***	n.s.	n.s.	n.s.									
P. mediterraneus	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	**	n.s.	n.s.	n.s.	n.s.								
R. centralis	n.s.	***	***	n.s.	n.s.	***	n.s.	n.s.	**	***	**	***	n.s.	n.s.	n.s.	n.s.	n.s.							
S. acuminata	n.s.	n.s.	n.s.	n.s.	***	**	**	***	**	n.s.	***	n.s.	*	***	***	***	***	***						
S. gracilis	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	**	***					
S. nemorensis	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	*	***	n.s.				
S. alacer	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.			
S. crassipes	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.		
S. linearis	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	**	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	
T. poseidonis	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	***	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

b.

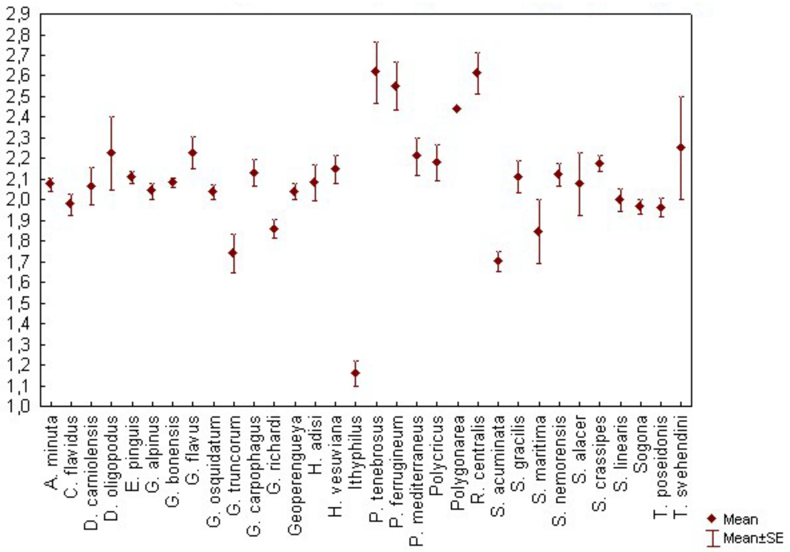
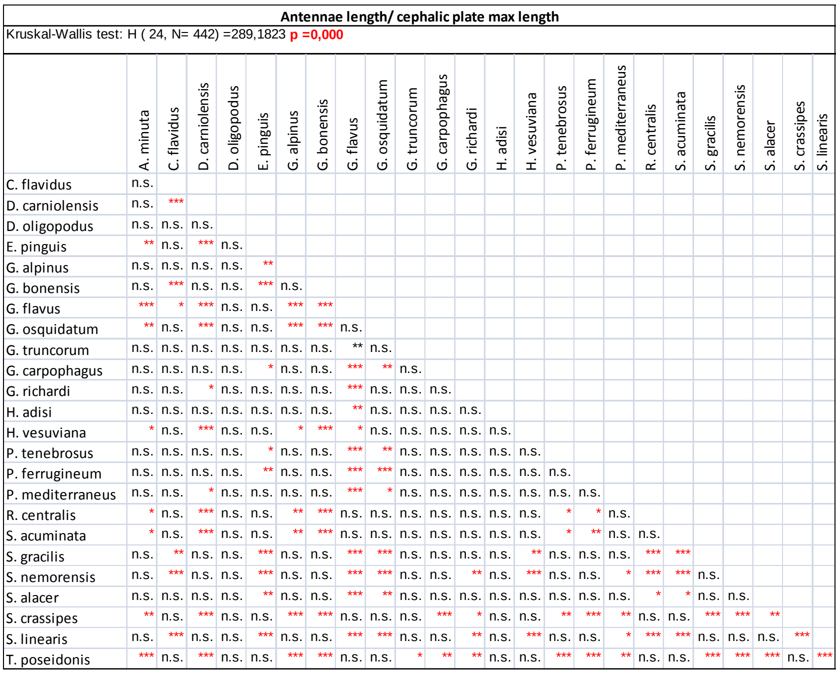


Fig. 3. A2. Analyses of the quantitative character “XIV antennal article: ratio of maximum length and maximum width ”: a. The results of a Kruskal–Wallis test were significant (H= 142,1926, P=0.000); the mean ranks of the ratio of maximum length and maximum width of the XIV antennal article are significantly different among the species (*=0,5-0,1; **=0,1-0,01; ***<0,01). b. Comparison of mean and standard error of the antennal distance grouped by species.

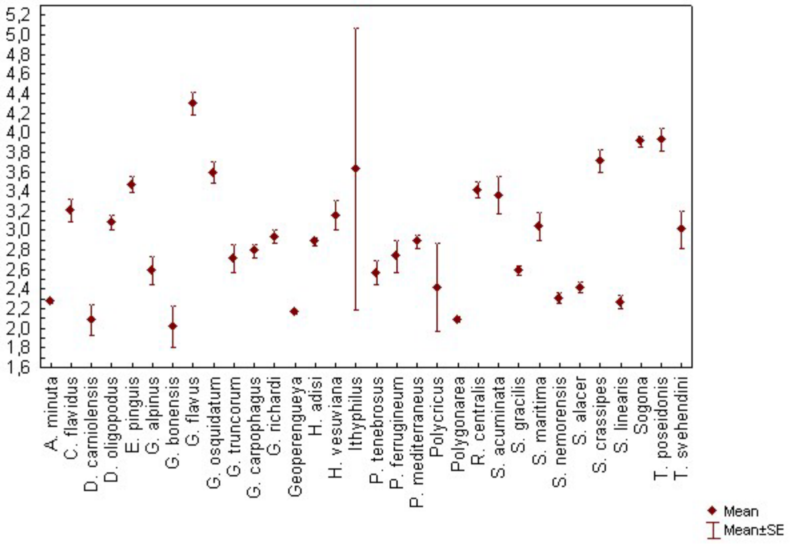
a.



Antennae length/ cephalic plate max length

Kruskal-Wallis test: H (24, N= 442) =289,1823 p =0,000

	A. minuta	C. flavidus	D. carniolensis	D. oligopodus	E. pinguis	G. alpinus	G. bonensis	G. flavus	G. osquidatum	G. truncorum	G. carpophagus	G. richardi	H. adisi	H. vesuviana	P. tenebrosus	P. ferrugineum	P. mediterraneus	R. centralis	S. acuminata	S. gracilis	S. nemorensis	S. alacer	S. crassipes	S. linearis
C. flavidus	n.s.																							
D. carniolensis	n.s.	***																						
D. oligopodus	n.s.	n.s.	n.s.																					
E. pinguis	**	n.s.	***	n.s.																				
G. alpinus	n.s.	n.s.	n.s.	n.s.	**																			
G. bonensis	n.s.	***	n.s.	n.s.	***	n.s.																		
G. flavus	***	*	***	n.s.	n.s.	***	***																	
G. osquidatum	**	n.s.	***	n.s.	n.s.	***	***	n.s.																
G. truncorum	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.															
G. carpophagus	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	***	**	n.s.														
G. richardi	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.													
H. adisi	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.												
H. vesuviana	*	n.s.	***	n.s.	n.s.	*	***	*	n.s.	n.s.	n.s.	n.s.	n.s.											
P. tenebrosus	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	***	**	n.s.	n.s.	n.s.	n.s.	n.s.										
P. ferrugineum	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	***	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.									
P. mediterraneus	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	***	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.								
R. centralis	*	n.s.	***	n.s.	n.s.	**	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	*	n.s.							
S. acuminata	*	n.s.	***	n.s.	n.s.	**	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	**	n.s.	n.s.						
S. gracilis	n.s.	**	n.s.	n.s.	***	n.s.	n.s.	***	***	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	***	***					
S. nemorensis	n.s.	***	n.s.	n.s.	***	n.s.	n.s.	***	***	n.s.	n.s.	**	n.s.	***	n.s.	n.s.	*	***	***	n.s.				
S. alacer	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	***	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	*	n.s.	n.s.			
S. crassipes	**	n.s.	***	n.s.	n.s.	***	***	n.s.	n.s.	n.s.	***	*	n.s.	n.s.	**	***	**	n.s.	n.s.	***	***	**		
S. linearis	n.s.	***	n.s.	n.s.	***	n.s.	n.s.	***	***	n.s.	n.s.	**	n.s.	***	n.s.	n.s.	*	***	***	n.s.	n.s.	n.s.	***	
T. poseidonis	***	n.s.	***	n.s.	n.s.	***	***	n.s.	n.s.	*	**	**	n.s.	n.s.	***	***	**	n.s.	n.s.	***	***	***	n.s.	***



b.

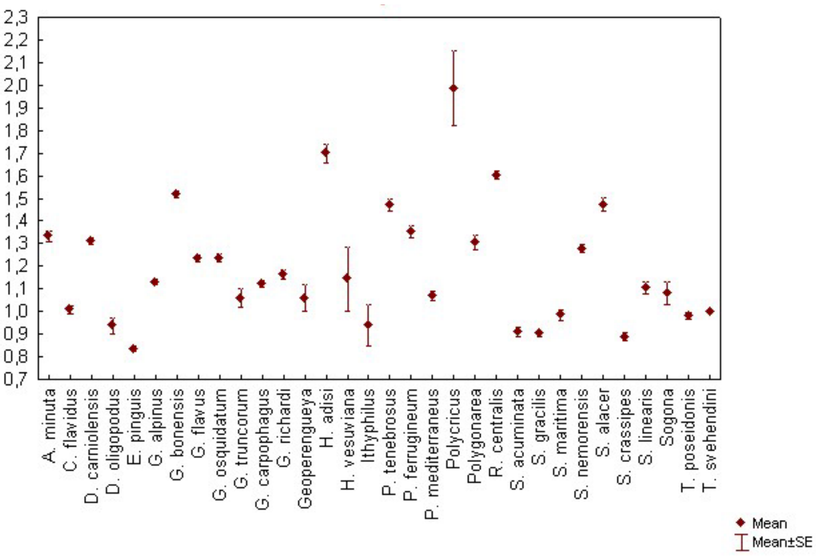
Fig. 4. A2. Analyses of the quantitative character "ratio of maximum length of the antenna and maximum length of cephalic plate": a .The results of a Kruskal–Wallis test were significant (H= 289,1823, P=0.000); the mean ranks of the ratio of the antennal maximum length and the cephalic plate maximum length are significantly different among the species (*=0,5-0,1; **=0,1-0,01; ***<0,01). b. Comparison of mean and standard error of the antennal distance grouped by species.

a.

Cephalic plate, max length/ max width

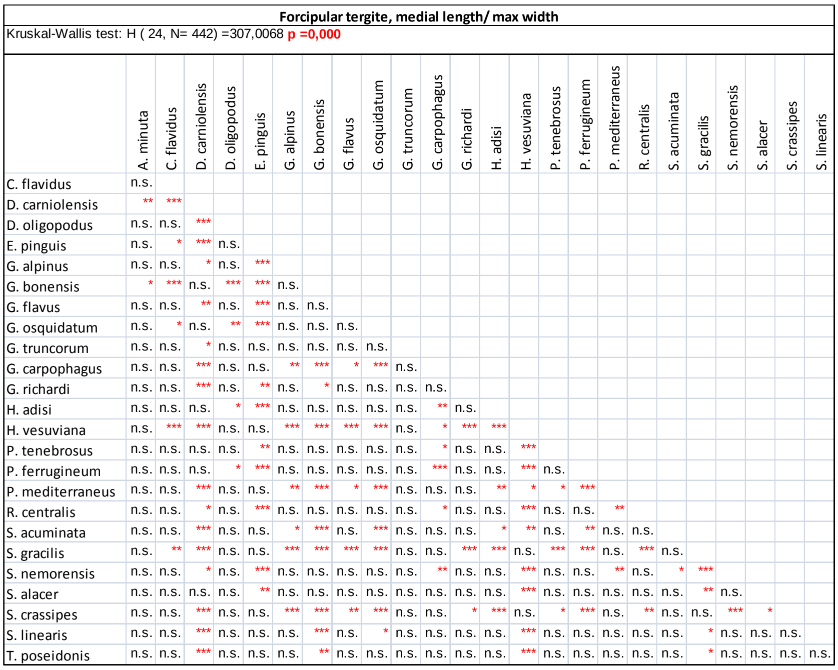
Kruskal-Wallis test: H (24, N= 442) =362,6414 p =0,000

	A. minuta	C. flavidus	D. carniolensis	D. oligopodus	E. pinguis	G. alpinus	G. bonensis	G. flavus	G. osquidatum	G. truncorum	G. carpophagus	G. richardi	H. adisi	H. vesuviana	P. tenebrosus	P. ferrugineum	P. mediterraneus	R. centralis	S. acuminata	S. gracilis	S. nemorensis	S. alacer	S. crassipes	S. linearis
C. flavidus	n.s.																							
D. carniolensis	n.s.	***																						
D. oligopodus	n.s.	n.s.	*																					
E. pinguis	***	n.s.	***	n.s.																				
G. alpinus	n.s.	n.s.	n.s.	n.s.	***																			
G. bonensis	n.s.	***	n.s.	***	***	***																		
G. flavus	n.s.	**	n.s.	n.s.	***	n.s.	n.s.																	
G. osquidatum	n.s.	**	n.s.	n.s.	***	n.s.	n.s.	n.s.																
G. truncorum	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.															
G. carpophagus	n.s.	n.s.	n.s.	n.s.	***	n.s.	***	n.s.	n.s.	n.s.														
G. richardi	n.s.	n.s.	n.s.	n.s.	***	n.s.	**	n.s.	n.s.	n.s.	n.s.													
H. adisi	n.s.	***	n.s.	***	***	**	n.s.	n.s.	n.s.	*	**	*												
H. vesuviana	*	n.s.	***	n.s.	n.s.	n.s.	***	***	***	n.s.	n.s.	*	***											
P. tenebrosus	n.s.	***	n.s.	**	***	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	***										
P. ferrugineum	n.s.	***	n.s.	**	***	*	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	***	n.s.									
P. mediterraneus	n.s.	n.s.	**	n.s.	**	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	**	***								
R. centralis	n.s.	***	n.s.	***	***	***	n.s.	*	*	**	***	***	n.s.	***	n.s.	n.s.	***							
S. acuminata	**	n.s.	***	n.s.	n.s.	**	***	***	***	n.s.	**	***	***	n.s.	***	***	n.s.	***						
S. gracilis	**	n.s.	***	n.s.	n.s.	***	***	***	***	n.s.	**	***	***	n.s.	***	***	*	***	n.s.					
S. nemorensis	n.s.	***	n.s.	*	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	*	n.s.	***	***				
S. alacer	n.s.	**	n.s.	*	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	*	n.s.	***	***	n.s.			
S. crassipes	**	n.s.	***	n.s.	n.s.	***	***	***	***	n.s.	**	***	***	n.s.	***	***	n.s.	***	n.s.	n.s.	***	***		
S. linearis	n.s.	n.s.	*	n.s.	***	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	*	**	n.s.	***	*	**	n.s.	n	**	
T. poseidonis	n.s.	n.s.	***	n.s.	n.s.	n.s.	***	**	**	n.s.	n.s.	n.s.	***	n.s.	***	***	n.s.	***	n.s.	n.s.	***	**	n.s.	n.s.



b.

Fig. 5. A2. Analyses of the quantitative character “cephalic plate: ratio of maximum length and maximum width ”: a. The results of a Kruskal–Wallis test were significant (H= 362,6414, P=0.000); the mean ranks of the ratio of maximum length and maximum width of the cephalic plate are significantly different among the species (*=0,5-0,1; **=0,1-0,01; ***<0,01). b. Comparison of mean and standard error of the antennal distance grouped by species.

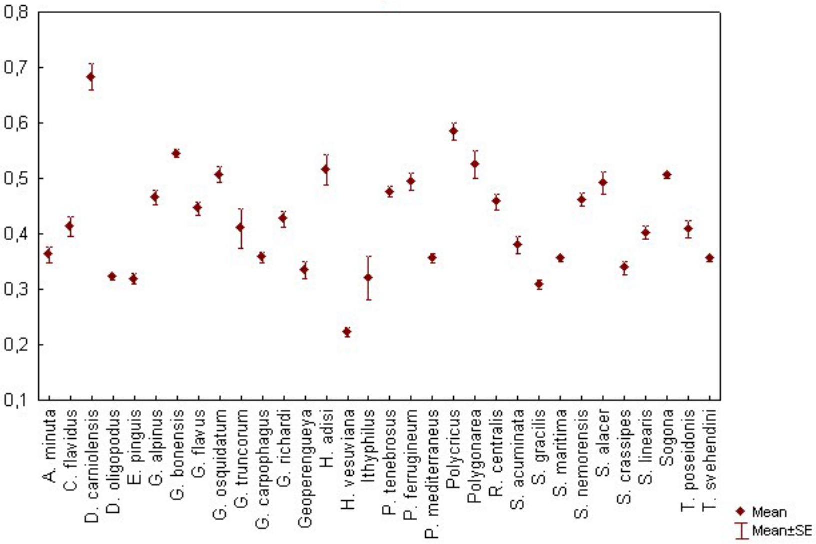


Forcipular tergite, medial length/ max width

Kruskal-Wallis test: H (24, N= 442) =307,0068 p =0,000

	A. minuta	C. flavidus	D. carniolensis	D. oligopodus	E. pinguis	G. alpinus	G. bonensis	G. flavus	G. osquidatum	G. truncorum	G. carpophagus	G. richardi	H. adisi	H. vesuviana	P. tenebrosus	P. ferrugineum	P. mediterraneus	R. centralis	S. acuminata	S. gracilis	S. nemorensis	S. alacer	S. crassipes	S. linearis
C. flavidus	n.s.																							
D. carniolensis	**	***																						
D. oligopodus	n.s.	n.s.	***																					
E. pinguis	n.s.	*	***	n.s.																				
G. alpinus	n.s.	n.s.	*	n.s.	***																			
G. bonensis	*	***	n.s.	***	***	n.s.																		
G. flavus	n.s.	n.s.	**	n.s.	***	n.s.	n.s.																	
G. osquidatum	n.s.	*	n.s.	**	***	n.s.	n.s.	n.s.																
G. truncorum	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.															
G. carpophagus	n.s.	n.s.	***	n.s.	n.s.	**	***	*	***	n.s.														
G. richardi	n.s.	n.s.	***	n.s.	**	n.s.	*	n.s.	n.s.	n.s.	n.s.													
H. adisi	n.s.	n.s.	n.s.	*	***	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.												
H. vesuviana	n.s.	***	***	n.s.	n.s.	***	***	***	***	n.s.	*	***	***											
P. tenebrosus	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	***										
P. ferrugineum	n.s.	n.s.	n.s.	*	***	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	***	n.s.									
P. mediterraneus	n.s.	n.s.	***	n.s.	n.s.	**	***	*	***	n.s.	n.s.	n.s.	**	*	*	***								
R. centralis	n.s.	n.s.	*	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	***	n.s.	n.s.	**							
S. acuminata	n.s.	n.s.	***	n.s.	n.s.	*	***	n.s.	***	n.s.	n.s.	n.s.	*	**	n.s.	**	n.s.	n.s.						
S. gracilis	n.s.	**	***	n.s.	n.s.	***	***	***	***	n.s.	n.s.	***	***	n.s.	***	***	n.s.	***	n.s.					
S. nemorensis	n.s.	n.s.	*	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	***	n.s.	n.s.	**	n.s.	*	***				
S. alacer	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.			
S. crassipes	n.s.	n.s.	***	n.s.	n.s.	***	***	**	***	n.s.	n.s.	*	***	n.s.	*	***	n.s.	**	n.s.	n.s.	***	*		
S. linearis	n.s.	n.s.	***	n.s.	n.s.	n.s.	***	n.s.	*	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	
T. poseidonis	n.s.	n.s.	***	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.

a.



b.

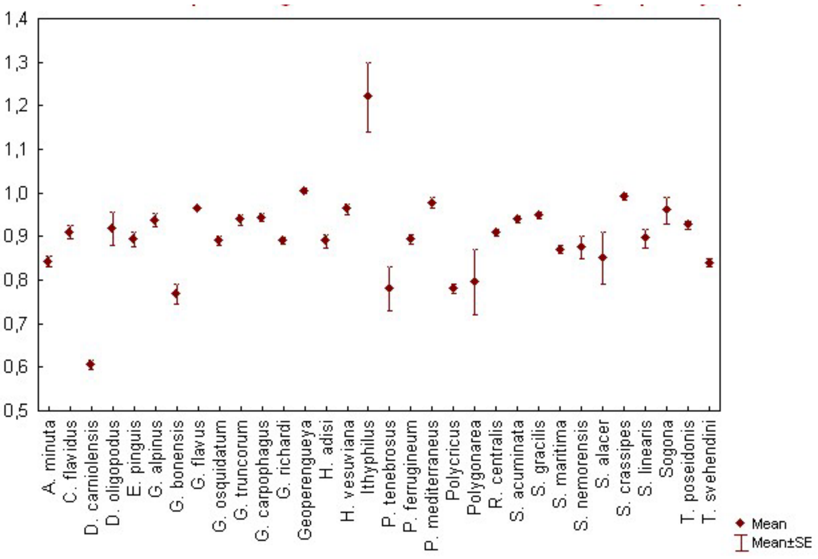
Fig. 6. A2. Analyses of the quantitative character “forcipular tergite: ratio of maximum length and maximum width ”: a. The results of a Kruskal–Wallis test were significant (H= 307,0068, P=0.000); the mean ranks of the ratio of maximum length and maximum width of the forcipular tergite are significantly different among the species (*=0,5-0,1; **=0,1-0,01; ***<0,01). b. Comparison of mean and standard error of the antennal distance grouped by species.

a.

Forcipular tergite max width/ T1 max width

Kruskal-Wallis test: H (24, N= 442) =221,8753 p =0,000

	A. minuta	C. flavidus	D. carniolensis	D. oligopodus	E. pinguis	G. alpinus	G. bonensis	G. flavus	G. osquidatum	G. truncorum	G. carpophagus	G. richardi	H. adisi	H. vesuviana	P. tenebrosus	P. ferrugineum	P. mediterraneus	R. centralis	S. acuminata	S. gracilis	S. nemorensis	S. alacer	S. crassipes	S. linearis
C. flavidus	n.s.																							
D. carniolensis	n.s.	***																						
D. oligopodus	n.s.	n.s.	n.s.																					
E. pinguis	n.s.	n.s.	***	n.s.																				
G. alpinus	n.s.	n.s.	***	n.s.	n.s.																			
G. bonensis	n.s.	**	n.s.	n.s.	n.s.	***																		
G. flavus	**	n.s.	***	n.s.	**	n.s.	***																	
G. osquidatum	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	***																
G. truncorum	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.															
G. carpophagus	n.s.	n.s.	***	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.														
G. richardi	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.													
H. adisi	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.												
H. vesuviana	*	n.s.	***	n.s.	*	n.s.	***	n.s.	***	n.s.	n.s.	***	*											
P. tenebrosus	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	***	n.s.	n.s.	**	n.s.	n.s.	***										
P. ferrugineum	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.									
P. mediterraneus	**	n.s.	***	n.s.	**	n.s.	***	n.s.	***	n.s.	n.s.	***	*	n.s.	***	***								
R. centralis	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	**							
S. acuminata	n.s.	n.s.	***	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.						
S. gracilis	*	n.s.	***	n.s.	n.s.	n.s.	***	n.s.	**	n.s.	n.s.	**	n.s.	n.s.	***	*	n.s.	n.s.	n.s.					
S. nemorensis	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	***	n.s.	n.s.	*				
S. alacer	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.			
S. crassipes	***	**	***	n.s.	***	*	***	n.s.	***	n.s.	n.s.	***	***	n.s.	***	***	n.s.	***	n.s.	n.s.	***	n.s.		
S. linearis	n.s.	n.s.	***	n.s.	n.s.	n.s.	*	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	***	
T. poseidonis	n.s.	n.s.	***	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.



b.

c.

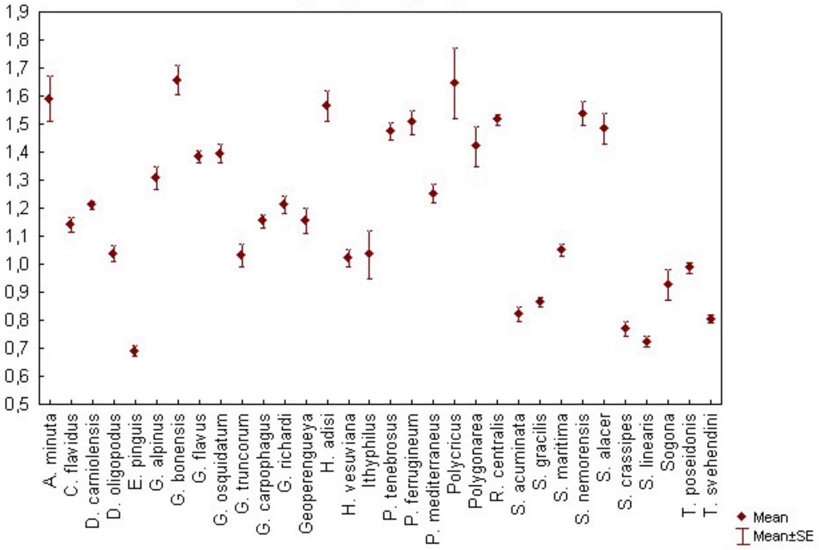
Fig. 7. A2. Analyses of the quantitative character “ratio of maximum width of forcipular tergite and maximum width of first tergite”: a. The results of a Kruskal–Wallis test were significant (H= 221,8753, P=0.000); the mean ranks of the ratio of the forcipular tergite maximum width and the first tergite (T1) maximum width are significantly different among the species (*=0,5-0,1; **=0,1-0,01; ***<0,01). b. Comparison of mean and standard error of the antennal distance grouped by species.

Forcipular segment, I article, max length/ max width

Kruskal-Wallis test: H (24, N= 442) =370,5559 p =0,000

	A. minuta	C. flavidus	D. carniolensis	D. oligopodus	E. pinguis	G. alpinus	G. bonensis	G. flavus	G. osquidatum	G. truncorum	G. carpophagus	G. richardi	H. adisi	H. vesuviana	P. tenebrosus	P. ferrugineum	P. mediterraneus	R. centralis	S. acuminata	S. gracilis	S. nemorensis	S. alacer	S. crassipes	S. linearis
C. flavidus	n.s.																							
D. carniolensis	n.s.	n.s.																						
D. oligopodus	n.s.	n.s.	n.s.																					
E. pinguis	***	***	***	n.s.																				
G. alpinus	n.s.	n.s.	n.s.	n.s.	***																			
G. bonensis	n.s.	***	**	*	***	n.s.																		
G. flavus	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.																	
G. osquidatum	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.																
G. truncorum	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.															
G. carpophagus	n.s.	n.s.	n.s.	n.s.	***	n.s.	***	n.s.	n.s.	n.s.														
G. richardi	n.s.	n.s.	n.s.	n.s.	***	n.s.	**	n.s.	n.s.	n.s.	n.s.													
H. adisi	n.s.	*	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	*	*	n.s.												
H. vesuviana	*	n.s.	n.s.	n.s.	n.s.	*	***	***	***	n.s.	n.s.	n.s.	***											
P. tenebrosus	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**										
P. ferrugineum	n.s.	**	*	n.s.	***	n.s.	n.s.	n.s.	n.s.	*	**	*	n.s.	***	n.s.									
P. mediterraneus	n.s.	n.s.	n.s.	n.s.	***	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.								
R. centralis	n.s.	***	*	*	***	n.s.	n.s.	n.s.	n.s.	*	**	*	n.s.	***	n.s.	n.s.	n.s.							
S. acuminata	***	*	***	n.s.	n.s.	***	***	***	***	n.s.	*	***	***	n.s.	***	***	***	***						
S. gracilis	***	n.s.	**	n.s.	n.s.	***	***	***	***	n.s.	*	**	***	n.s.	***	***	***	***	n.s.					
S. nemorensis	n.s.	***	*	n.s.	***	n.s.	n.s.	n.s.	n.s.	*	***	*	n.s.	***	n.s.	n.s.	n.s.	n.s.	***	***				
S. alacer	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	***	***	n.s.			
S. crassipes	***	**	***	n.s.	n.s.	***	***	***	***	n.s.	**	***	***	n.s.	***	***	***	***	n.s.	n.s.	***	***		
S. linearis	***	***	***	n.s.	n.s.	***	***	***	***	n.s.	***	***	***	n.s.	***	***	***	***	n.s.	n.s.	***	***	n.s.	
T. poseidonis	*	n.s.	n.s.	n.s.	n.s.	*	***	***	***	n.s.	n.s.	n.s.	***	n.s.	**	***	n.s.	***	n.s.	n.s.	***	*	n.s.	n.s.

a.



b.

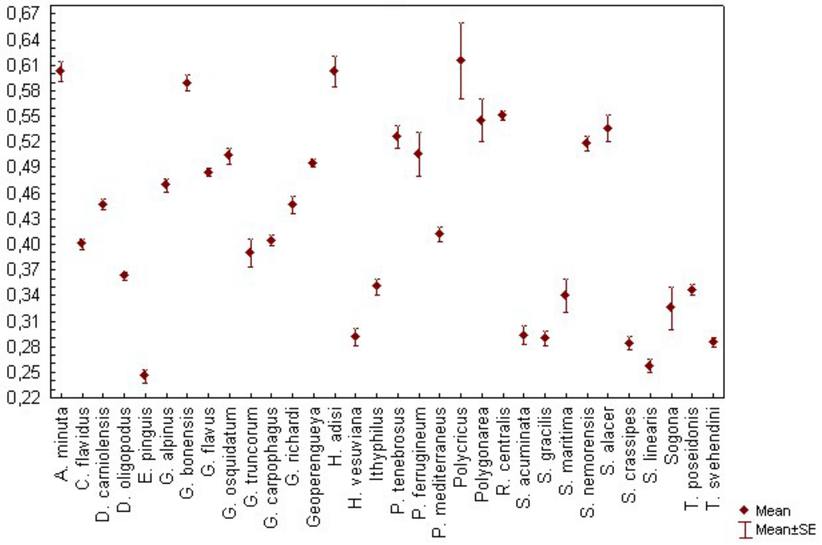
Fig. 8. A2. Analyses of the quantitative character "first article of forcipular segment: ratio of maximum length and maximum width ": a. The results of a Kruskal–Wallis test were significant (H= 370,5559, P=0.000); the mean ranks of the ratio of the first article of the forcipular segment maximum length and maximum width are significantly different among the species (*=0,5-0,1; **=0,1-0,01; ***<0,01). b. Comparison of mean and standard error of the antennal distance grouped by species.

Forcipular segment, I article length/coxosternum width

Kruskal-Wallis test: H (24, N= 442) =383,0102 **p =0,000**

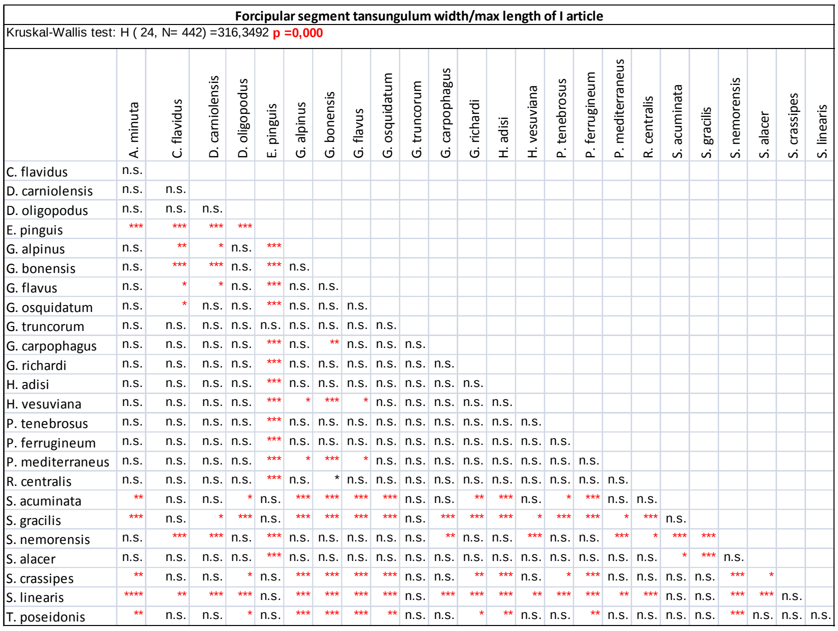
	A. minuta	C. flavidus	D. carniolensis	D. oligopodus	E. pinguis	G. alpinus	G. bonensis	G. flavus	G. osquidatum	G. truncorum	G. carpophagus	G. richardi	H. adisi	H. vesuviana	P. tenebrosus	P. ferrugineum	P. mediterraneus	R. centralis	S. acuminata	S. gracilis	S. nemorensis	S. alacer	S. crassipes	S. linearis
C. flavidus	*																							
D. carniolensis	n.s.	n.s.																						
D. oligopodus	n.s.	n.s.	n.s.																					
E. pinguis	***	**	***	n.s.																				
G. alpinus	n.s.	n.s.	n.s.	n.s.	***																			
G. bonensis	n.s.	***	**	**	***	n.s.																		
G. flavus	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.																	
G. osquidatum	n.s.	**	n.s.	n.s.	***	n.s.	n.s.	n.s.																
G. truncorum	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.															
G. carpophagus	*	n.s.	n.s.	n.s.	***	n.s.	***	n.s.	*	n.s.														
G. richardi	n.s.	n.s.	n.s.	n.s.	***	n.s.	**	n.s.	n.s.	n.s.	n.s.													
H. adisi	n.s.	***	n.s.	*	***	n.s.	n.s.	n.s.	n.s.	*	**	n.s.												
H. vesuviana	***	n.s.	***	n.s.	n.s.	***	***	***	***	n.s.	n.s.	***	***											
P. tenebrosus	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***										
P. ferrugineum	n.s.	**	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	***	n.s.									
P. mediterraneus	n.s.	n.s.	n.s.	n.s.	***	n.s.	***	n.s.	*	n.s.	n.s.	n.s.	**	*	n.s.	*								
R. centralis	n.s.	***	n.s.	*	***	n.s.	n.s.	n.s.	n.s.	n.s.	***	*	n.s.	***	n.s.	n.s.	***							
S. acuminata	***	n.s.	***	n.s.	n.s.	***	***	***	***	n.s.	n.s.	***	***	n.s.	***	***	*	***						
S. gracilis	***	n.s.	***	n.s.	n.s.	***	***	***	***	n.s.	*	***	***	n.s.	***	***	*	***	n.s.					
S. nemorensis	n.s.	**	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	***	n.s.	n.s.	**	n.s.	***	***				
S. alacer	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	***	***	n.s.			
S. crassipes	***	*	***	n.s.	n.s.	***	***	***	***	n.s.	*	***	***	n.s.	***	***	**	***	n.s.	n.s.	***	***		
S. linearis	***	**	***	n.s.	n.s.	***	***	***	***	n.s.	**	***	***	n.s.	***	***	***	***	n.s.	n.s.	***	***	n.s.	
T. poseidonis	**	n.s.	n.s.	n.s.	n.s.	*	***	**	***	n.s.	n.s.	n.s.	***	n.s.	**	***	n.s.	***	n.s.	n.s.	***	*	n.s.	n.s.

a.



b.

Fig. 9. A2. Analyses of the quantitative character “ratio of maximum length of first article of forcipular length and maximum width of coxosternum”: a. The results of a Kruskal–Wallis test were significant (H= 383,0102, P=0.000); the mean ranks of the ratio of the first article of forcipular segment maximum length and the coxosternum maximum width are significantly different among the species (*=0,5-0,1; **=0,1-0,01; ***<0,01). b. Comparison of mean and standard error of the antennal distance grouped by species.

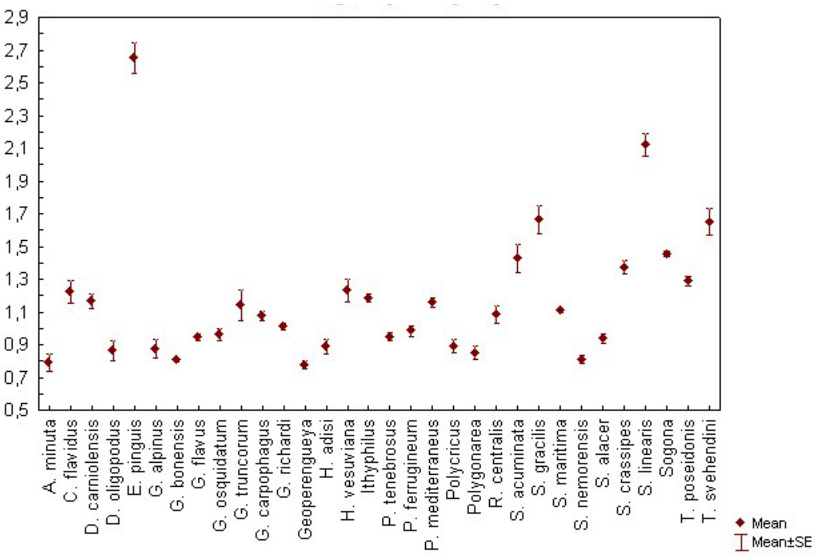


a.

Forcipular segment tansungulum width/max length of I article

Kruskal-Wallis test: H (24, N= 442) =316,3492 p =0,000

	A. minuta	C. flavidus	D. carniolensis	D. oligopodus	E. pinguis	G. alpinus	G. bonensis	G. flavus	G. osquidatum	G. truncorum	G. carpophagus	G. richardi	H. adisi	H. vesuviana	P. tenebrosus	P. ferrugineum	P. mediterraneus	R. centralis	S. acuminata	S. gracilis	S. nemorensis	S. alacer	S. crassipes	S. linearis
C. flavidus	n.s.																							
D. carniolensis	n.s.	n.s.																						
D. oligopodus	n.s.	n.s.	n.s.																					
E. pinguis	***	***	***	***																				
G. alpinus	n.s.	**	*	n.s.	***																			
G. bonensis	n.s.	***	***	n.s.	***	n.s.																		
G. flavus	n.s.	*	*	n.s.	***	n.s.	n.s.																	
G. osquidatum	n.s.	*	n.s.	n.s.	***	n.s.	n.s.	n.s.																
G. truncorum	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.															
G. carpophagus	n.s.	n.s.	n.s.	n.s.	***	n.s.	**	n.s.	n.s.	n.s.														
G. richardi	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.													
H. adisi	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.												
H. vesuviana	n.s.	n.s.	n.s.	n.s.	***	*	***	*	n.s.	n.s.	n.s.	n.s.	n.s.											
P. tenebrosus	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.										
P. ferrugineum	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.									
P. mediterraneus	n.s.	n.s.	n.s.	n.s.	***	*	***	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.								
R. centralis	n.s.	n.s.	n.s.	n.s.	***	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.							
S. acuminata	**	n.s.	n.s.	*	n.s.	***	***	***	***	n.s.	n.s.	**	***	n.s.	*	***	n.s.	n.s.						
S. gracilis	***	n.s.	*	***	n.s.	***	***	***	***	n.s.	***	***	***	*	***	***	*	***	n.s.					
S. nemorensis	n.s.	***	***	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	***	n.s.	n.s.	***	*	***	***				
S. alacer	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	***	n.s.			
S. crassipes	**	n.s.	n.s.	*	n.s.	***	***	***	***	n.s.	n.s.	**	***	n.s.	*	***	n.s.	n.s.	n.s.	n.s.	***	*		
S. linearis	****	**	***	***	n.s.	***	***	***	***	n.s.	***	***	***	**	***	***	**	***	n.s.	n.s.	***	***	n.s.	
T. poseidonis	**	n.s.	n.s.	*	n.s.	***	***	***	**	n.s.	n.s.	*	**	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.



b.

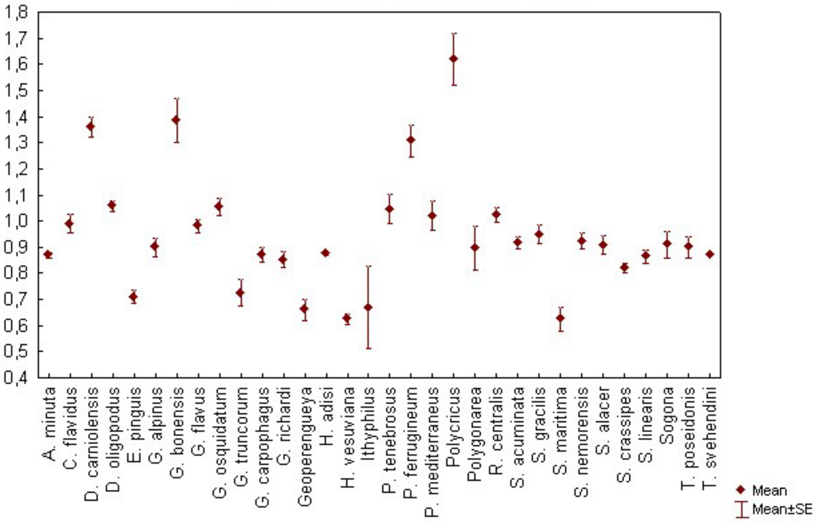
Fig. 10. A2. Analyses of the quantitative character "ratio of maximum length of the tarsungulum and maximum length of the first article of forcipular segment ": a. The results of a Kruskal–Wallis test were significant (H= 316,3492, P=0.000); the mean ranks of the ratio of the tarsungulum of forcipular segment maximum length and the first article of forcipular segment maximum length are significantly different among the species (*=0,5-0,1; **=0,1-0,01; ***<0,01). b. Comparison of mean and standard error of the antennal distance grouped by species.

Last leg bearing segment, metatergite max length/ max width

Kruskal-Wallis test: H (24, N= 442) =241,8480 p =0,000

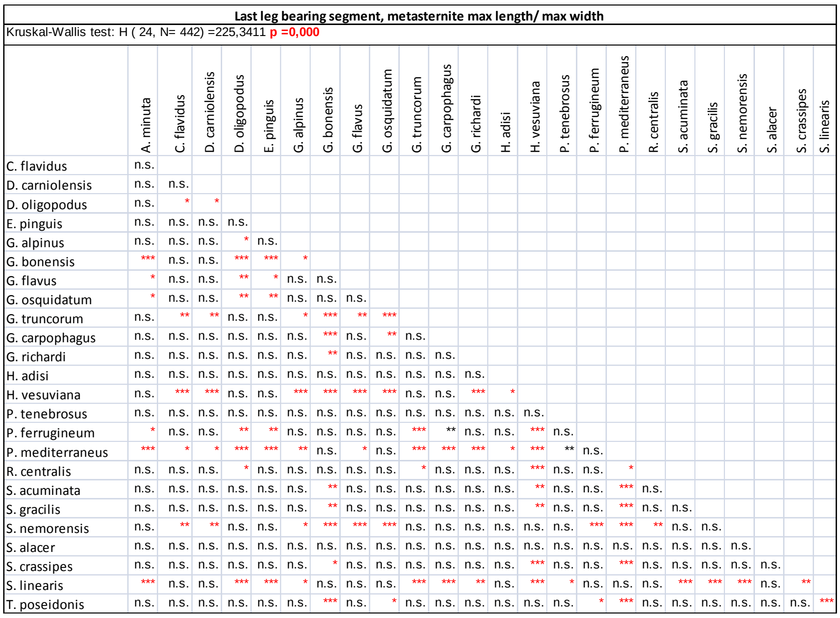
	A. minuta	C. flavidus	D. carniolensis	D. oligopodus	E. pinguis	G. alpinus	G. bonensis	G. flavus	G. osquidatum	G. truncorum	G. carpophagus	G. richardi	H. adisi	H. vesuviana	P. tenebrosus	P. ferrugineum	P. mediterraneus	R. centralis	S. acuminata	S. gracilis	S. nemorensis	S. alacer	S. crassipes	S. linearis
C. flavidus	n.s.																							
D. carniolensis	*	**																						
D. oligopodus	n.s.	n.s.	n.s.																					
E. pinguis	n.s.	***	***	*																				
G. alpinus	n.s.	n.s.	***	n.s.	n.s.																			
G. bonensis	*	*	n.s.	n.s.	***	***																		
G. flavus	n.s.	n.s.	**	n.s.	***	n.s.	*																	
G. osquidatum	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.																
G. truncorum	n.s.	n.s.	***	n.s.	n.s.	n.s.	***	n.s.	*															
G. carpophagus	n.s.	n.s.	***	n.s.	n.s.	n.s.	***	n.s.	*	n.s.														
G. richardi	n.s.	n.s.	***	n.s.	n.s.	n.s.	***	n.s.	**	n.s.	n.s.													
H. adisi	n.s.	n.s.	***	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.												
H. vesuviana	n.s.	***	***	***	n.s.	**	***	***	***	n.s.	**	n.s.	n.s.											
P. tenebrosus	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***										
P. ferrugineum	n.s.	n.s.	n.s.	n.s.	***	***	n.s.	*	n.s.	***	***	***	**	***	n.s.									
P. mediterraneus	n.s.	n.s.	**	n.s.	***	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	*								
R. centralis	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.							
S. acuminata	n.s.	n.s.	***	n.s.	*	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	***	n.s.	n.s.						
S. gracilis	n.s.	n.s.	***	n.s.	**	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	**	n.s.	n.s.	n.s.					
S. nemorensis	n.s.	n.s.	***	n.s.	*	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	***	n.s.	n.s.	n.s.	n.s.				
S. alacer	n.s.	n.s.	*	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.			
S. crassipes	n.s.	*	***	n.s.	n.s.	n.s.	***	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	*	*	n.s.	n.s.	n.s.	n.s.		
S. linearis	n.s.	n.s.	***	n.s.	n.s.	n.s.	***	n.s.	*	n.s.	n.s.	n.s.	n.s.	*	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
T. poseidonis	n.s.	n.s.	***	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

a.



b.

Fig. 11. A2. Analyses of the quantitative character “metatergite f the last leg-bearing segment: ratio of maximum length and maximum width ”: a. The results of a Kruskal–Wallis test were significant (H= 241,8480, P=0.000); the mean ranks of the ratio of the metatergite of the last leg bearing segment maximum length and maximum width are significantly different among the species (*=0,5-0,1; **=0,1-0,01; ***<0,01). b. Comparison of mean and standard error of the antennal distance grouped by species.

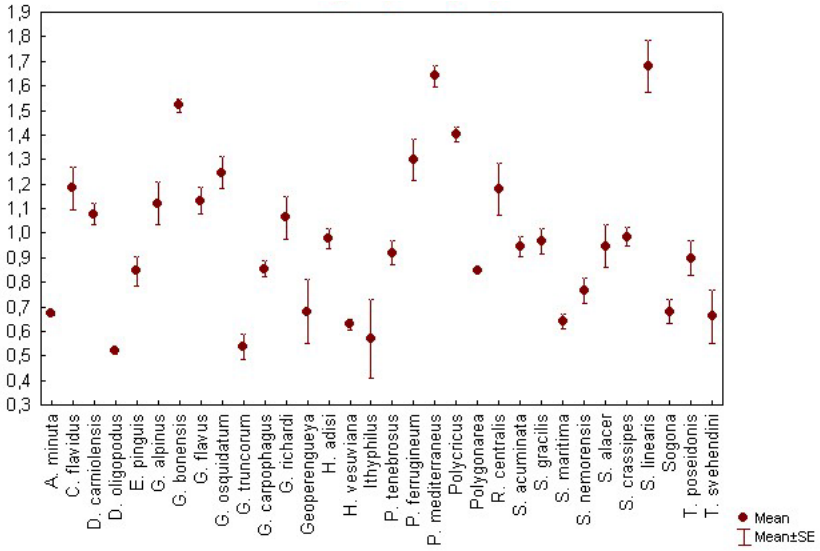


Last leg bearing segment, metasternite max length/ max width

Kruskal-Wallis test: H (24, N= 442) =225,3411 p =0,000

	A. minuta	C. flavidus	D. carniolensis	D. oligopodus	E. pinguis	G. alpinus	G. bonensis	G. flavus	G. osquidatum	G. truncorum	G. carpophagus	G. richardi	H. adisi	H. vesuviana	P. tenebrosus	P. ferrugineum	P. mediterraneus	R. centralis	S. acuminata	S. gracilis	S. nemorensis	S. alacer	S. crassipes	S. linearis
C. flavidus	n.s.																							
D. carniolensis	n.s.	n.s.																						
D. oligopodus	n.s.	*	*																					
E. pinguis	n.s.	n.s.	n.s.	n.s.																				
G. alpinus	n.s.	n.s.	n.s.	*	n.s.																			
G. bonensis	***	n.s.	n.s.	***	***	*																		
G. flavus	*	n.s.	n.s.	**	*	n.s.	n.s.																	
G. osquidatum	*	n.s.	n.s.	**	**	n.s.	n.s.	n.s.																
G. truncorum	n.s.	**	**	n.s.	n.s.	*	***	**	***															
G. carpophagus	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	**	n.s.														
G. richardi	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.													
H. adisi	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.												
H. vesuviana	n.s.	***	***	n.s.	n.s.	***	***	***	***	n.s.	n.s.	***	*											
P. tenebrosus	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.										
P. ferrugineum	*	n.s.	n.s.	**	**	n.s.	n.s.	n.s.	n.s.	***	**	n.s.	n.s.	***	n.s.									
P. mediterraneus	***	*	*	***	***	**	n.s.	*	n.s.	***	***	***	*	***	**	n.s.								
R. centralis	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	***	n.s.	n.s.	*							
S. acuminata	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	***	n.s.						
S. gracilis	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	***	n.s.	n.s.					
S. nemorensis	n.s.	**	**	n.s.	n.s.	*	***	***	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	***	**	n.s.	n.s.				
S. alacer	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.			
S. crassipes	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.		
S. linearis	***	n.s.	n.s.	***	***	*	n.s.	n.s.	n.s.	***	***	**	n.s.	***	*	n.s.	n.s.	n.s.	***	***	***	n.s.	**	
T. poseidonis	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***

a.



b.

Fig. 12. A2. Analyses of the quantitative character “metasternite of the last leg-bearing segment: ratio of maximum length and maximum width ”: a. The results of a Kruskal–Wallis test were significant (H= 225,3411, P=0.000); the mean ranks of the ratio of the metasternite of the last leg bearing segment maximum length and maximum width are significantly different among the species (*=0,5-0,1; **=0,1-0,01; ***<0,01). b. Comparison of mean and standard error of the antennal distance grouped by species.

a.

Last leg bearing segment, coxa max length/ max width

Kruskal-Wallis test: H (24, N= 442) =267,8352 p =0,000

	A. minuta	C. flavidus	D. carniolensis	D. oligopodus	E. pinguis	G. alpinus	G. bonensis	G. flavus	G. osquidatum	G. truncorum	G. carpophagus	G. richardi	H. adisi	H. vesuviana	P. tenebrosus	P. ferrugineum	P. mediterraneus	R. centralis	S. acuminata	S. gracilis	S. nemorensis	S. alacer	S. crassipes	S. linearis
C. flavidus	n.s.																							
D. carniolensis	n.s.	n.s.																						
D. oligopodus	n.s.	n.s.	n.s.																					
E. pinguis	n.s.	**	**	*																				
G. alpinus	n.s.	n.s.	n.s.	n.s.	n.s.																			
G. bonensis	n.s.	n.s.	n.s.	n.s.	***	***																		
G. flavus	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**																	
G. osquidatum	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.																
G. truncorum	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.															
G. carpophagus	n.s.	***	***	**	n.s.	n.s.	***	*	***	n.s.														
G. richardi	n.s.	***	***	*	n.s.	n.s.	***	n.s.	**	n.s.	n.s.													
H. adisi	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	***	**												
H. vesuviana	*	***	***	***	n.s.	**	***	***	***	n.s.	n.s.	n.s.	***											
P. tenebrosus	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	***	**	n.s.	***										
P. ferrugineum	n.s.	n.s.	n.s.	n.s.	***	***	n.s.	**	n.s.	*	***	***	n.s.	***	n.s.									
P. mediterraneus	n.s.	n.s.	n.s.	n.s.	***	***	n.s.	***	*	**	***	***	n.s.	***	n.s.	n.s.								
R. centralis	n.s.	n.s.	n.s.	n.s.	***	**	n.s.	*	n.s.	*	***	***	n.s.	***	n.s.	n.s.	n.s.							
S. acuminata	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	*	n.s.	n.s.	***	n.s.	**	***	**						
S. gracilis	n.s.	**	**	n.s.	n.s.	n.s.	***	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	*	***	***	***	n.s.					
S. nemorensis	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	**	n.s.	n.s.	***	n.s.	*	***	n.s.	n.s.	n.s.				
S. alacer	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.			
S. crassipes	n.s.	**	***	*	n.s.	n.s.	***	n.s.	*	n.s.	n.s.	n.s.	*	n.s.	*	***	***	***	n.s.	n.s.	n.s.	n.s.		
S. linearis	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	***	***	***	n.s.	n.s.	n.s.	n.s.	n.s.	
T. poseidonis	n.s.	*	*	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	***	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

b.

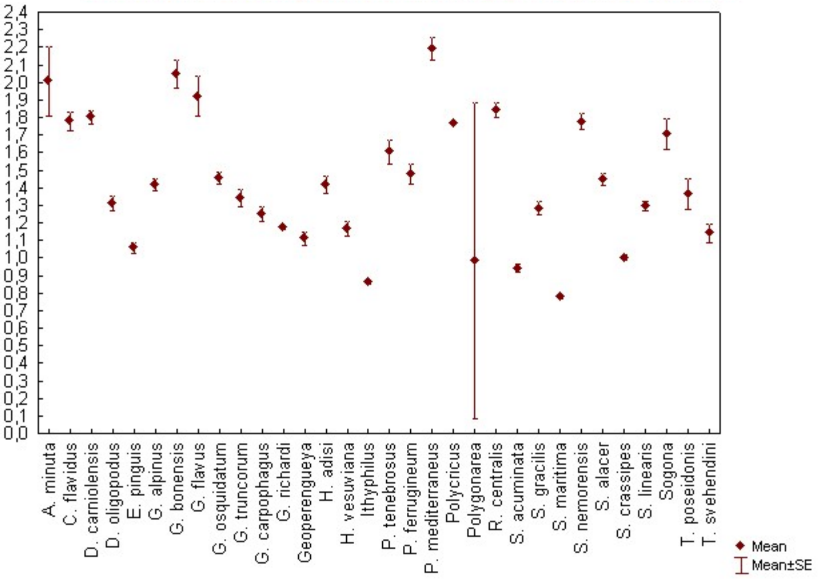
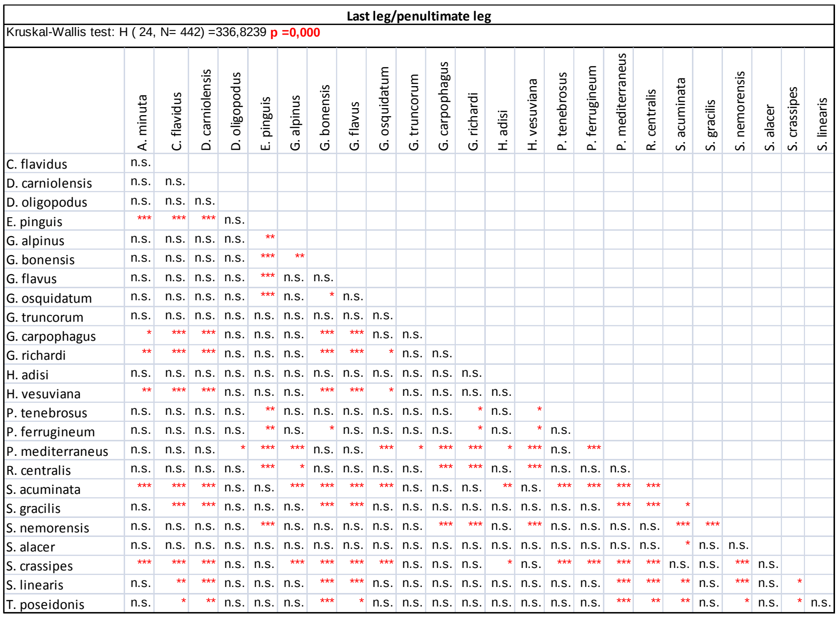


Fig. 13. A2. Analyses of the quantitative character “coxa of the last leg-bearing segment: ratio of maximum length and maximum width ”: a. The results of a Kruskal–Wallis test were significant (H= 267,8352, P=0.000); the mean ranks of the ratio of the coxa of the last leg bearing segment maximum length and maximum width are significantly different among the species (*=0,5-0,1; **=0,1-0,01; ***<0,01). b. Comparison of mean and standard error of the antennal distance grouped by species.

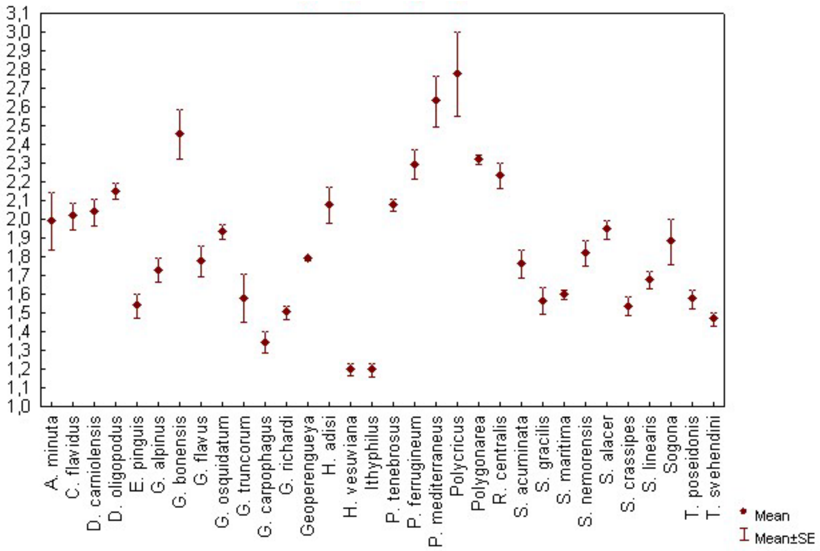


Last leg/penultimate leg

Kruskal-Wallis test: H (24, N= 442) =336,8239 **p =0,000**

	A. minuta	C. flavidus	D. carniolensis	D. oligopodus	E. pinguis	G. alpinus	G. bonensis	G. flavus	G. osquidatum	G. truncorum	G. carpophagus	G. richardi	H. adisi	H. vesuviana	P. tenebrosus	P. ferrugineum	P. mediterraneus	R. centralis	S. acuminata	S. gracilis	S. nemorensis	S. alacer	S. crassipes	S. linearis
C. flavidus	n.s.																							
D. carniolensis	n.s.	n.s.																						
D. oligopodus	n.s.	n.s.	n.s.																					
E. pinguis	***	***	***	n.s.																				
G. alpinus	n.s.	n.s.	n.s.	n.s.	**																			
G. bonensis	n.s.	n.s.	n.s.	n.s.	***	**																		
G. flavus	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.																	
G. osquidatum	n.s.	n.s.	n.s.	n.s.	***	n.s.	*	n.s.																
G. truncorum	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.															
G. carpophagus	*	***	***	n.s.	n.s.	n.s.	***	***	n.s.	n.s.														
G. richardi	**	***	***	n.s.	n.s.	n.s.	***	***	*	n.s.	n.s.													
H. adisi	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.												
H. vesuviana	**	***	***	n.s.	n.s.	n.s.	***	***	*	n.s.	n.s.	n.s.	n.s.											
P. tenebrosus	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	*										
P. ferrugineum	n.s.	n.s.	n.s.	n.s.	**	n.s.	*	n.s.	n.s.	n.s.	n.s.	*	n.s.	*	n.s.									
P. mediterraneus	n.s.	n.s.	n.s.	*	***	***	n.s.	n.s.	***	*	***	***	*	***	n.s.	***								
R. centralis	n.s.	n.s.	n.s.	n.s.	***	*	n.s.	n.s.	n.s.	n.s.	***	***	n.s.	***	n.s.	n.s.	n.s.							
S. acuminata	***	***	***	n.s.	n.s.	***	***	***	***	n.s.	n.s.	n.s.	**	n.s.	***	***	***	***						
S. gracilis	n.s.	***	***	n.s.	n.s.	n.s.	***	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	***	*					
S. nemorensis	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	***	***	n.s.	***	n.s.	n.s.	n.s.	n.s.	***	***				
S. alacer	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.			
S. crassipes	***	***	***	n.s.	n.s.	***	***	***	***	n.s.	n.s.	n.s.	*	n.s.	***	***	***	***	n.s.	n.s.	***	n.s.		
S. linearis	n.s.	**	***	n.s.	n.s.	n.s.	***	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	***	**	n.s.	***	n.s.	*	
T. poseidonis	n.s.	*	**	n.s.	n.s.	n.s.	***	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	**	**	n.s.	*	n.s.	*	n.s.

a.



b.

Fig. 14. A2. Analyses of the quantitative character "ratio of maximum length of last leg and maximum length of penultimate leg": a. The results of a Kruskal–Wallis test were significant (H= 336,8239, P=0.000); the mean ranks of the ratio of the last leg maximum length and penultimate leg maximum width are significantly different among the species (*=0,5-0,1; **=0,1-0,01; ***<0,01). b. Comparison of mean and standard error of the antennal distance grouped by species.

The poison calyx of Geophilomorpha centipedes (Chilopoda): comparative morphology and evolution

Abstract

Geophilomorphs are a rich, diverse clade, comprising more than 1200 described species. They are the dominant predators in most of the soil interstitial ecosystems throughout the world. However, available knowledge on venom apparatus for this group is so far very inadequate, limited to very few species and the structure of the poison duct had rarely been studied. Here I describe the poison calyx of 16 species of geophilomorphs, using different microscopic techniques, including confocal laser scanning microscopy. I found a great variation in position and shape of the venom glands among the species considered. Then I reconstruct the evolutionary changes of these traits against a phylogeny of Geophilomorpha. Reconstructing evolutionary processes accounting for their diversity can provide basic information to understand the diversity of the ecological role of geophilomorphs in soil ecosystems.

Introduction

Chilopods are an ecologically important arthropod group of soil and leaf litter predators.

The prey is immobilized or killed by injecting venom from the poison glands, located in the first modified pair of trunk legs which are incorporated into the complex of food-manipulating appendages as a pair of maxillipedes (or forcipules). This modified pair of appendages is one of the unambiguous autapomorphic characters of Chilopoda identified by Dohle (1985). Each forcipule consists of four articles: trochanteropefemur, femur, tibia and tarsungulum. In Geophilomorpha, all articles may be provided with teeth, frequently on the trochanteroprefemur and at the base of the tarsungulum (fig.1).

Newport (1844) was the first author to recognise that the forcipules of centipedes contain a poison gland.

The venom is secreted through a pore located at a short distance from the tip of the claw; the pore is connected through a chitinous venom duct, the poison duct, to the poriferous region, the poison calyx.

The internal part of the poison duct is surrounded by the numerous glandular units of the poison gland (Rosenberg et al. 2011).

The venom glands of Chilopoda can be regarded as invaginations of the cuticle containing a high number of epidermal sub-glands, that consisting of four different cell types, a secretory cell, an intermediary cell, and two different canal cells (Rosenberg & Hilken, 2006).

Light and electron-microscopy studies described the ultra-structure of the poison glands of *Lithobius forficatus* (Rosenberg and Hilken, 2006) and some scolopendromorphs (*Scolopendra morsitans*: Dass and Jangi, 1978; *Ethmostigmus rubripes*: Ménez et al., 1990; *Cryptops iheringi*, *Otostigmus pradoi*, *S. viridicornis*: Antoniazzi et al., 2009).

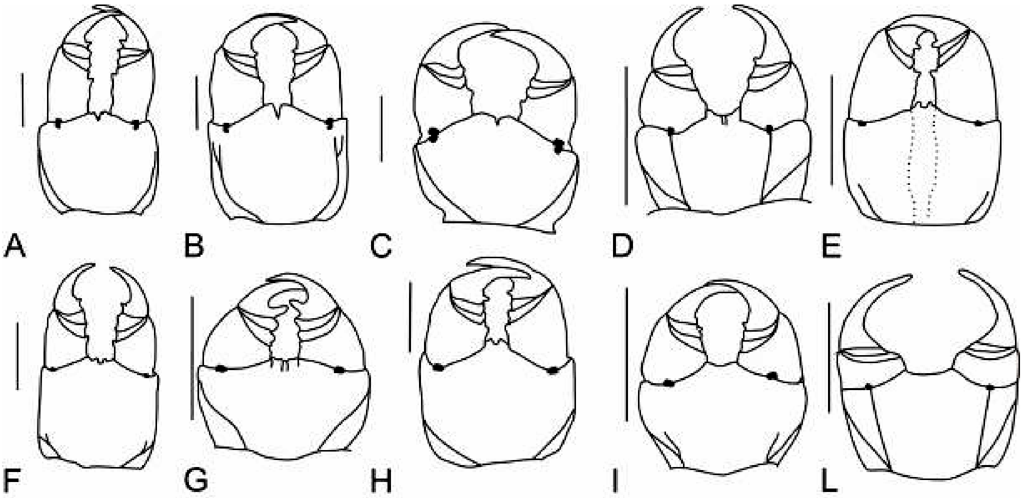


Fig. 1. Forcipular segment and forcipules of some geophilomorphs (all Geophilidae s.l.), ventral view (scale 0,5mm). A. *Steneurytion antipodum.* B. *Pachymerium ferrugineum.* C. *Zelanophilus provocator.* D. *Tuoba poseidonis.* E. *Alloschizotaenia minuta.* F. *Pleurogeophilus mediterraneus.* G. *Strigamia crassipes.* H. *Polygonarea* sp. I. *Geophilus richardi.* L. *Stenotaenia linearis.*

Size, shape and placement of poison calyx vary among chilopod species.

In Scutigeromorpha, Lithobiomorpha and Craterostigmomorpha, the venom gland is elongate and situated distally in the maxilliped, in the distal half of the trochanteroprefemur along the outer curvature of the maxilliped (Chao and Chang, 2006; Edgecombe and Giribet, 2008; Edgecombe and Barrow, 2007; Rosenberg and Hilken, 2006). The calyx is generally more or less cylindrical.

Also in Geophilomorpha, glands are cylindrical, in schendylids and mecistophalids (Hoffman and Pereira, 1991; Foddai et al., 2003; Bonato et al., 2006) and mostly contained in the trochanteroprefemur; in some geophilids, Foddai and Minelli (1999) described calyxes bush- or lampbrush-like in shape.

A classification of the possible shapes of the poison calyx, admittedly referring mainly to scolopendromorphs, was introduced by Chao & Chen

(2006), who distinguished these shapes as either short cylindrical, or long elongated cylindrical, sub-cordate, round or bell-bottomed; various is also the position of the internal end of the duct, which may reach either the tarsungulum, the femur, the tibia, the trocantheroprefemur or the coxosternum. Very peculiar are two geophilomorphs *Henia (Chaetechelyne) vesuviana* (Dignathodontidae) and *Aphilodon angustatus* (Aphilodontidae), the venom glands are placed in the trunk between the 12th and 18th segment (Duboscq, 1896) and between the 15th and 23rd segment (Pereira et al., 2007), respectively.

Aspects of the venom apparatus of a limited number of taxa of geophilomorphs have been described: Chao & Chen (2006) contributed to the knowledge of the poison ducts of *Strigamia maritima* (Leach, 1817, *sub Scolioplanes maritima japonicus*) (Geophilidae), *Stigmatogaster japonica* Takakuwa, 1935 (Himantariidae), *Taiwanella yanagiharai* Takakuwa, 1936, *Mecistocephalus smithi* Pocock, 1895 and *Mecistocephalus mikado* Attems, 1928 (Mecistocephalidae: Mecistocephalinae) and *Prolamnonyx holstii* (Pocock, 1919) (Mecistocephalidae: Arrupinae); Lewis (1996) described the poison calyx of *Ribautia arabica* (Geophilidae), Bonato et al. (2006) *Eurygeophilus multistiliger* and *E. pinguis* (Geophilidae); Pereira et al. (2007) *Schendylops inquilinus* (Schendylidae), *Aphilodon angustatus* (Aphilodontidae); Uliana et al. (2007) described those of some mecistocephalids of the Japanese and Taiwanese islands; few poison ducts were been illustrated (Takakuwa 1940a, b, 1941, Lewis 1999, 2002, Bonato et al. 2002, Foddai et al. 2003).

More data from different genera of geophilids are needed to reconstruct the evolution of the poison duct and the phylogenetic relationships within this order.

In this work, I investigated comparatively the morphology of the poison calyx of 16 species of geophilomorphs. I interpret the diversity in morphology of venom glands upon a phylogenetic scenario, to explore evolutionary patterns and trends accounting for the observed diversity, and to control for phylogenetic effects in evaluating ecological correlates of different feeding life forms.

Materials and methods

The poison calyx of 16 species of Geophilomorpha was examined (tab. 1). These species represent 6 families: Geophilidae, Mecistocephalidae, Linotaeniidae, Dignathodontidae, Schendylidae, Himantariidae.

All specimens examined were adult and collected in the field by me and belonging to the Minelli-Bonato collection, Dipartimento di Biologia, Università di Padova.

species
Mecistocephalidae
Dicellophilus carniolensis (C.L. Koch, 1847)
Himantariidae
Stigmatogaster gracilis (Meinert, 1870)
Schendylidae
Schendyla nemorensis (C.L. Koch, 1837)
Dignathodontidae
Henia (Chaetechelyne) vesuviana (Newport, 1845)
Henia (Meinertia) bicarinata (Meinert, 1870)
Henia (Henia) illyrica (Meinert, 1870)
Linotaeniidae
Strigamia crassipes (C.L. Koch, 1835)
Geophilidae
Clinopodes flavidus C.L. Koch, 1847
Geophilus alpinus Meinert, 1870
Geophilus carpophagus Leach, 1815
Geophilus flavus (De Geer, 1778)
Geophilus truncorum Bergsøe & Meinert, 1866
Pachymerium ferrugineum (C.L. Koch, 1835)
Pleurogeophilus mediterraneus (Meinert, 1870)
Stenotaenia linearis (C.L. Koch, 1835)
Tuoba poseidonis (Verhoeff, 1901)

Tab. 1. Species of Geophilomorpha examined

Examination

To analyze position and shape of the poison calyx, the specimens were examined by light microscopy (Leica DMLB).

To avoid the possible ontogenetic variation, only adult specimens were used.

The mouth parts of one specimens of each species were dissected and the left forcipula was taken away. To observe the structure of the poison calyx, internal soft tissues were digested with KOH 5% at 60°C for 4 h at least: this method allowed to remove soft tissues and leave the exoskeleton intact. The remaining cuticle was bleached with acid acetic, washed with distilled water, then the sample was mounted in glycerol. In the mounting process care was paid to prevent deformation (compression or crushing) using spacers between slide and coverslip. Preparations were examined under different microscopic techniques, exploiting the effect of the autoflorescence of the cuticle. Specimens were studied with a Leica DM5000B microscope, using bright field light or differential interference contrast (DIC). Picture were acquired with a Leica DFC 300 FX camera using Leica Application Suite software. Some digested specimens were also observed with confocal laser scanning microscopy (CLSM) Leica DMI 6000B, equipped with Leica TCS SP5 unit, with 543 nm Helium/Neon laser and 550-680 nm emission filter (CSLM). Optical sections were taken at a pace of 0,17 lm and analyzed with ImageJ (version 1.42).

Results

Length of poison calyx varied among species (tab. 2). The poison duct may be limited to the tarsungulum, or extend into the third (tibia), second (femur) or first article (trochanteroprefemur) of the forcipule, or even into the coxosternum and, in the only case of *Henia vesuviana,* into the trunk (figs. 2, 3, 4).

species	Ta	Ti	Fe	Tr	Co
Mecistocephalidae					
Dicellophilus carniolensis	p	p	p	p	a
Himantariidae					
Stigmatogaster gracilis	p	p	p	p	a
Schendylidae					
Schendyla nemorensis	p	p	a	a	a
Dignathodontidae					
Henia (Chaetechelyne) vesuviana	a	a	a	a	a
Henia (Meinertia) bicarinata	a	p	p	a	a
Henia (Henia) illyrica	a	a	a	p	a
Linotaeniidae					
Strigamia crassipes	a	a	a	p	a
Geophilidae					
Clinopodes flavidus	p	p	p	a	a
Geophilus alpinus	a	p	p	a	a
Geophilus carpophagus	a	p	p	a	a
Geophilus flavus	a	p	p	a	a
Geophilus truncorum	a	a	p	p	a
Pachymerium ferrugineum	a	p	p	a	a
Pleurogeophilus mediterraneus	a	p	p	a	a
Stenotaenia linearis	p	p	p	p	a
Tuoba poseidonis	a	p	p	a	a

Tab. 2. Position of the poison calyx in the different species examined. Ta: tarsungulum, Ti: tibia, Fe: femur, Tr: trochanteroprefemur, Co: coxosternum; a: absent; p: present.

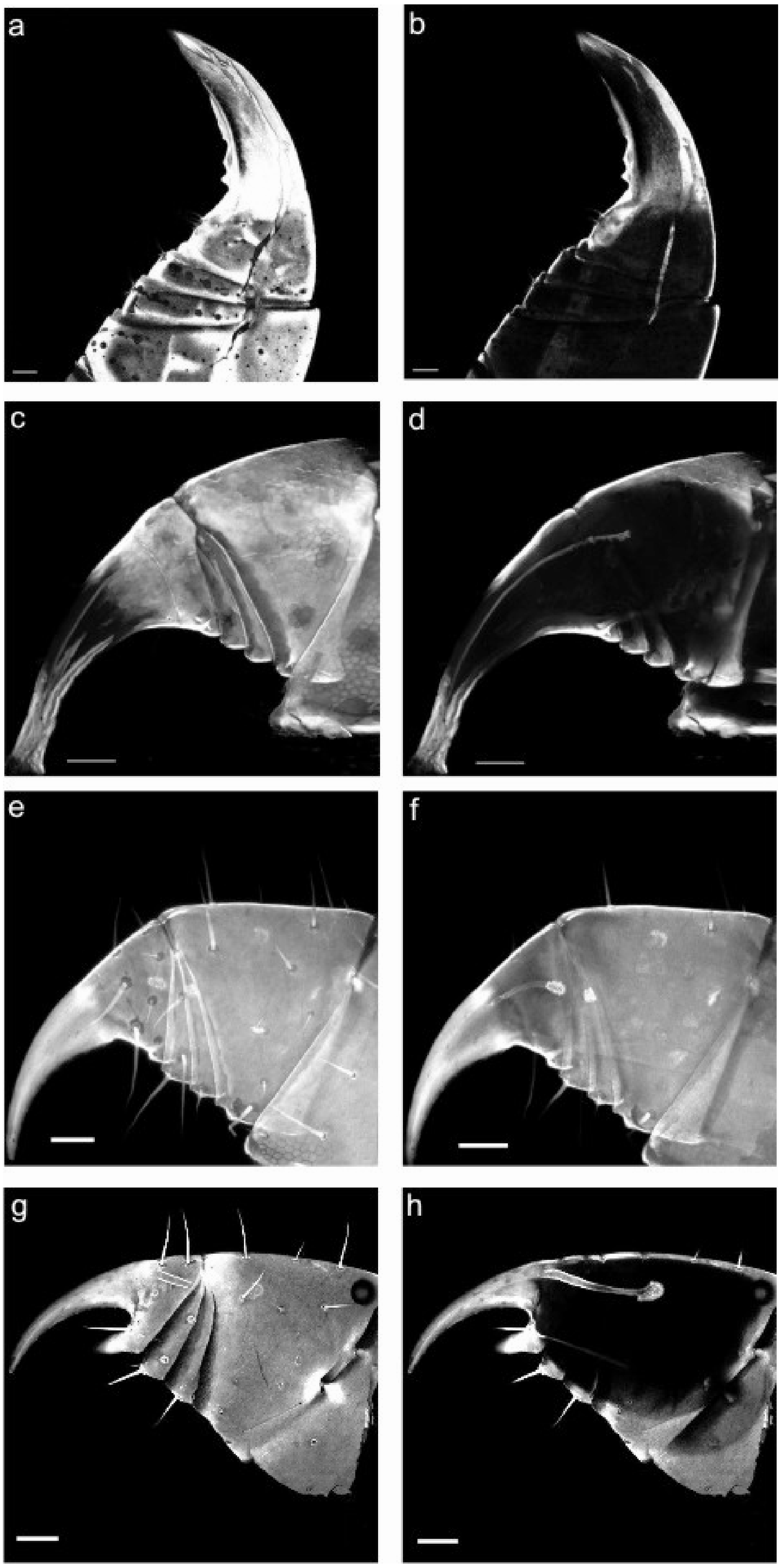


Fig. 2. Forcipule and poison ducts in Geophilomorpha. CSLM images. I. a), b) *Dicellophilus carniolensis.* c), d) *Stigmatogaster gracilis*. e), f) *Schendyla nemorensis*. g), h) *Strigamia crassipes.* Scale bar 100 µm.

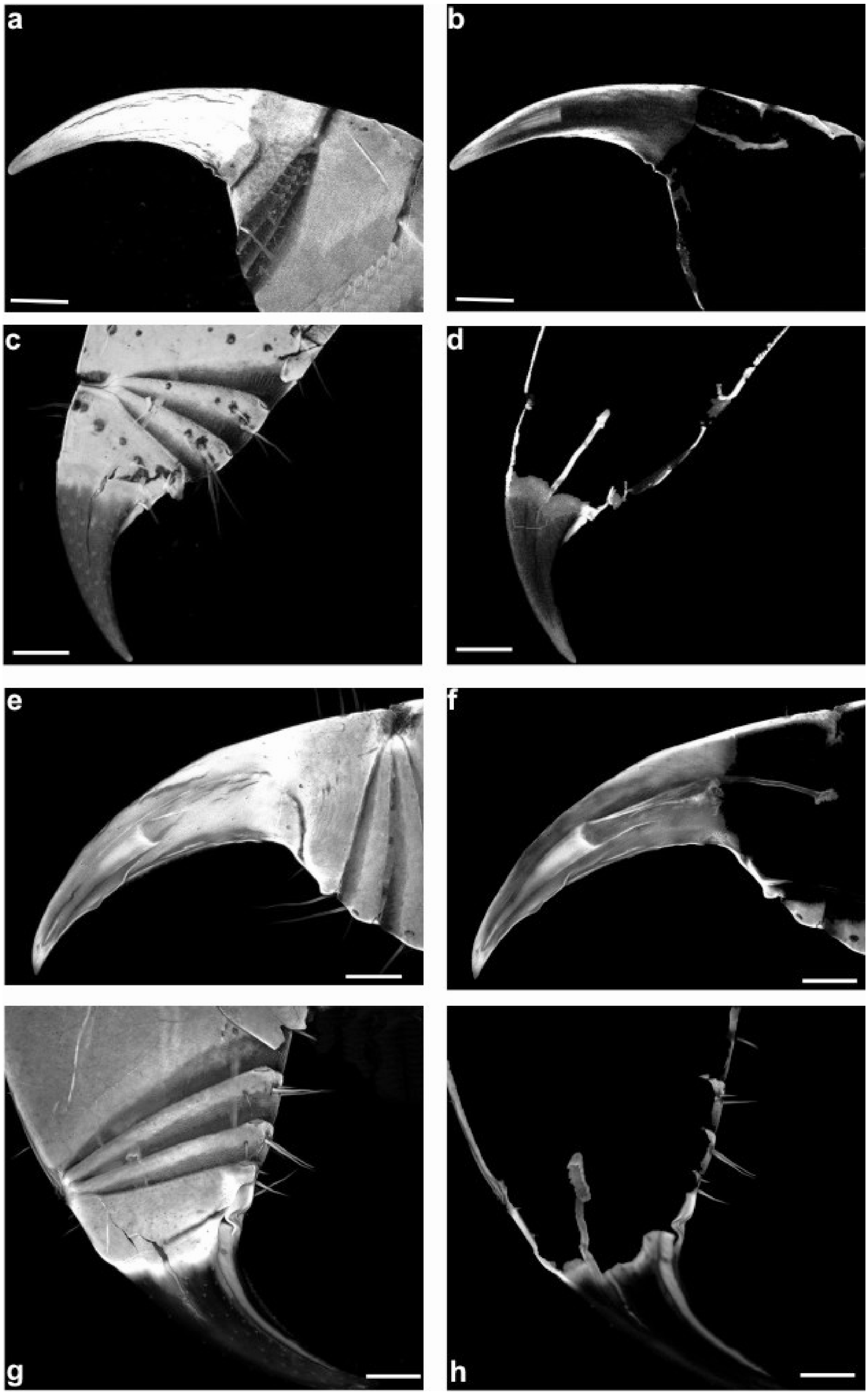


Fig. 3. Forcipule and poison ducts in Geophilidae. CSLM images. II. a), b) *Stenotaenia linearis.* c), d) *Pachymerium ferrugineum*. e), f) *Pleurogeophilus mediterraneus*. g), h) *Clinopodes flavidus.* Scale bar 100 μm.

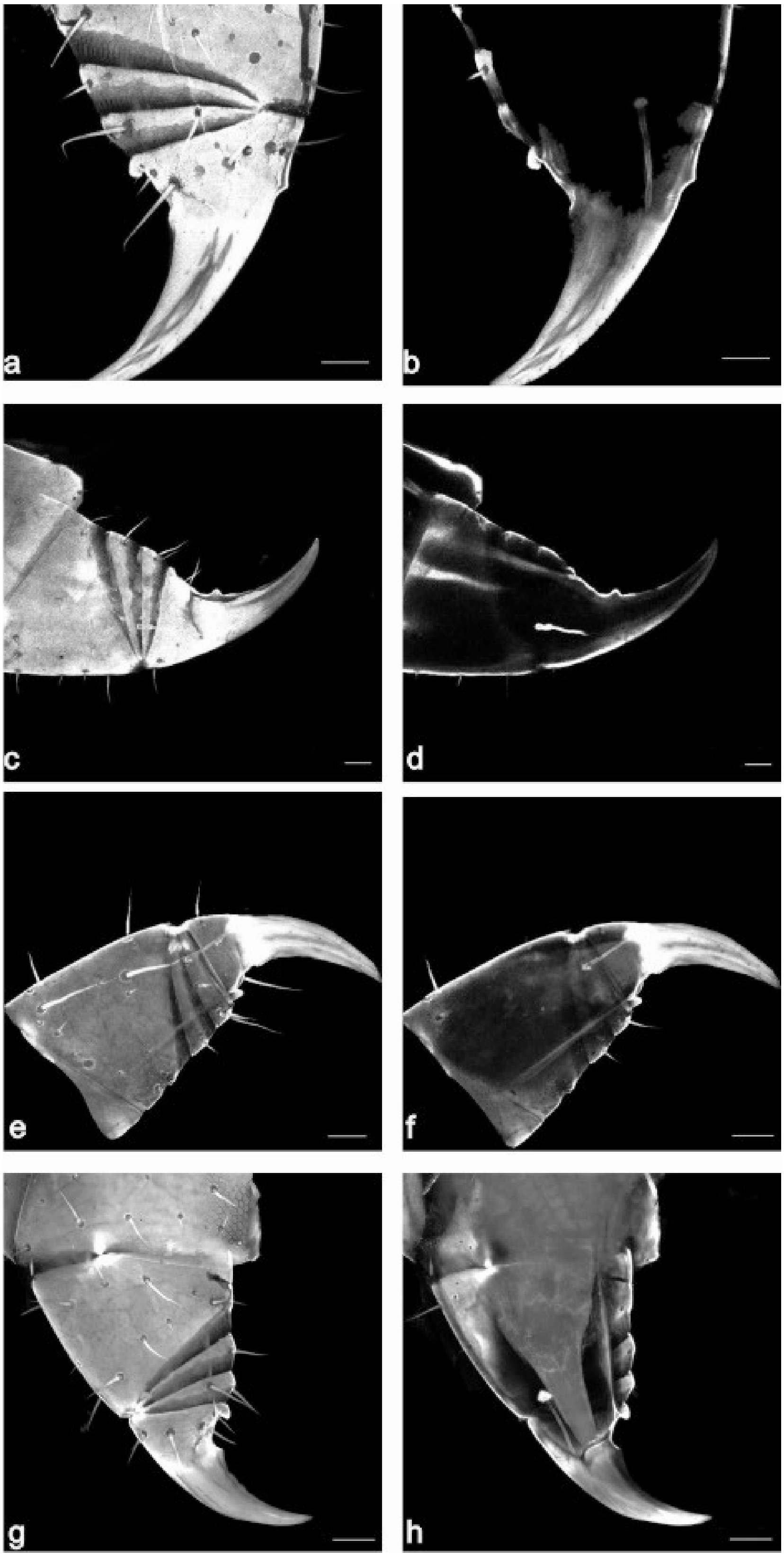


Fig. 4. Forcipule and poison ducts in Geophilidae. CSLM images. III. a), b) *Geophilus alpinus.* c), d) *Geophilus carpophagus*. e), f) *Geophilus flavus*. g), h) *Geophilus truncorum.* Scale bar 50 µm.

In addition to the length, other characteristic of poison duct varied among the species examined. The poison duct can be straight (*D. carniolensis*, *T. poseidonis*, *P. ferrugineum*) or curved (*S. gracilis, S. nemorensis, S. crassipes, P. mediterraneus, C. flavidus*) (figs. 2-3). In most species, the duct runs along the outer edge of tarsungulum for the distal part then in the middle at the end of tarsungulum; in other species (*D. carniolensis, P. mediterraneus, P. ferrugineum*) the duct runs in the middle for its full length.

Shapes of the poison calyx varied among species considered (fig. 5).

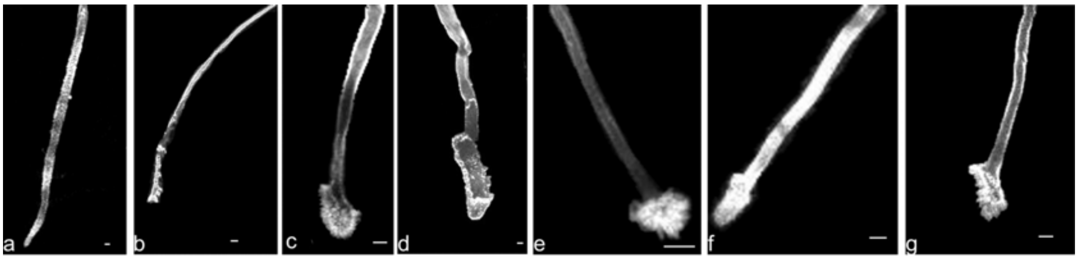


Fig. 5. Poison calyx of some Geophilomorpha, CSLM images: a) *Dicellophilus carniolensis*; b) *Stigmatogaster gracilis*; c) *Strigamia crassipes*; d) *Clinopodes flavidus*; e) *Geophilus truncorum*; f) *Pachymerium ferrugineum*; g) *Pleurogeophilus mediterraneus*. Scale bar 10 µm.

The poison calyx can be cylindrical, sub-cordate, round, bell bottomed, bush- and lampbrush- like in shape; furthermore the calyx can be symmetrical or not symmetrical (tab 3, figs. 6 -7-8 -9).

species	**shape**	
Mecistocephalidae		
Dicellophilus carniolensis	cylindrical	symmetrical
Himantariidae		
Stigmatogaster gracilis	cylindrical	symmetrical
Schendylidae		
Schendyla nemorensis	lampbrush-like	symmetrical
Dignathodontidae		
Henia (Chaetechelyne) vesuviana	round	symmetrical
Henia (Meinertia) bicarinata	sub-cordate	asymmetrical
Henia (Henia) illyrica	lampbrush-like	symmetrical
Linotaeniidae		
Strigamia crassipes	round	asymmetrical
Geophilidae		
Clinopodes flavidus	bell-bottomed	asymmetrical
Geophilus alpinus	round	symmetrical
Geophilus carpophagus	sub-cordate	symmetrical
Geophilus flavus	sub-cordate	symmetrical
Geophilus truncorum	bush-like	symmetrical
Pachymerium ferrugineum	sub-cordate	symmetrical
Pleurogeophilus mediterraneus	lampbrush-like	asymmetrical
Stenotaenia linearis	bell-bottomed	asymmetrical
Tuoba poseidonis	bush-like	symmetrical

Tab. 3. Shape of the poison calyx in the examined species

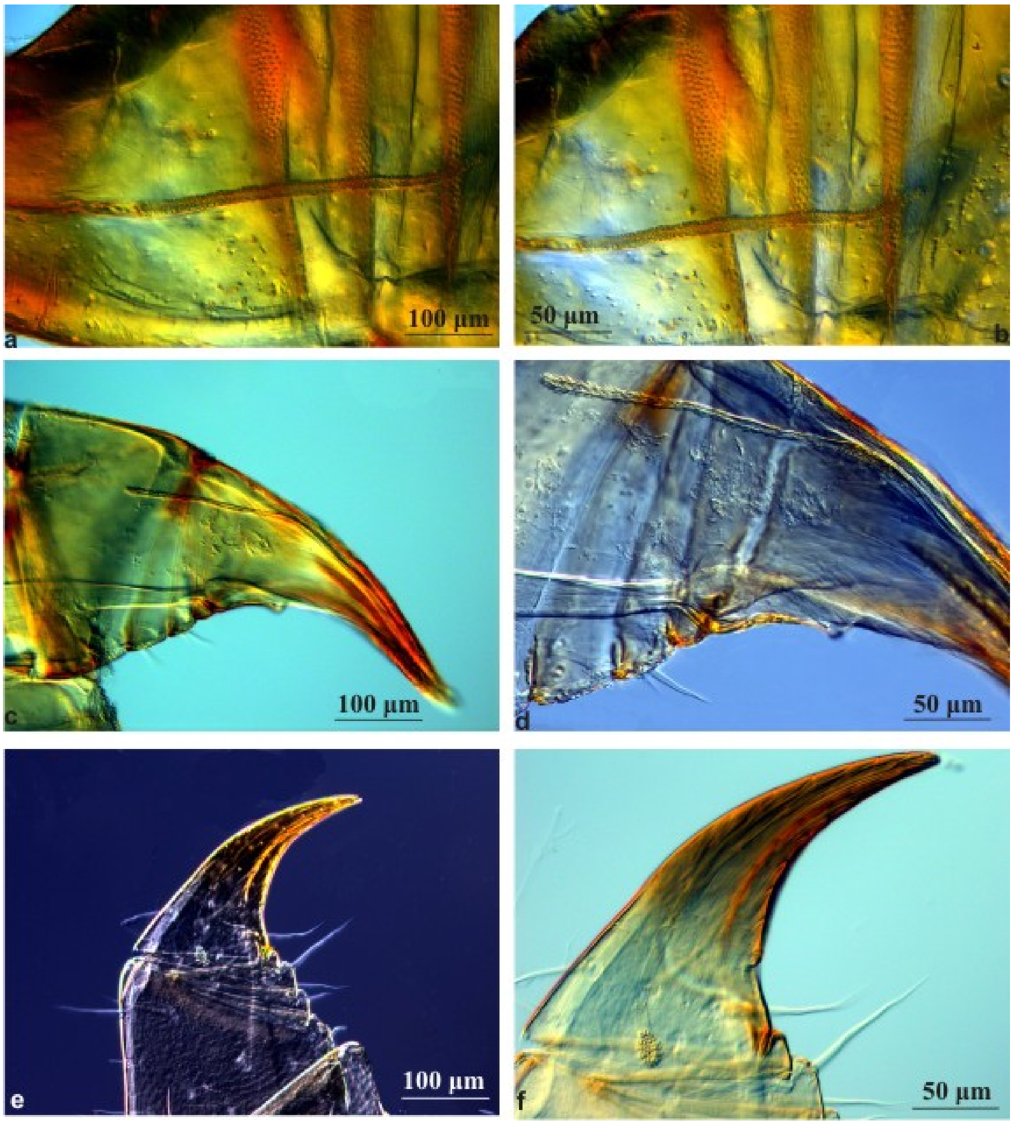


Fig. 6. Poison ducts in Geophilomorpha. DIC images. I. a), b) *Dicellophilus carniolensis.* c), d) *Stigmatogaster gracilis* e), f) *Schendyla nemorensis*.

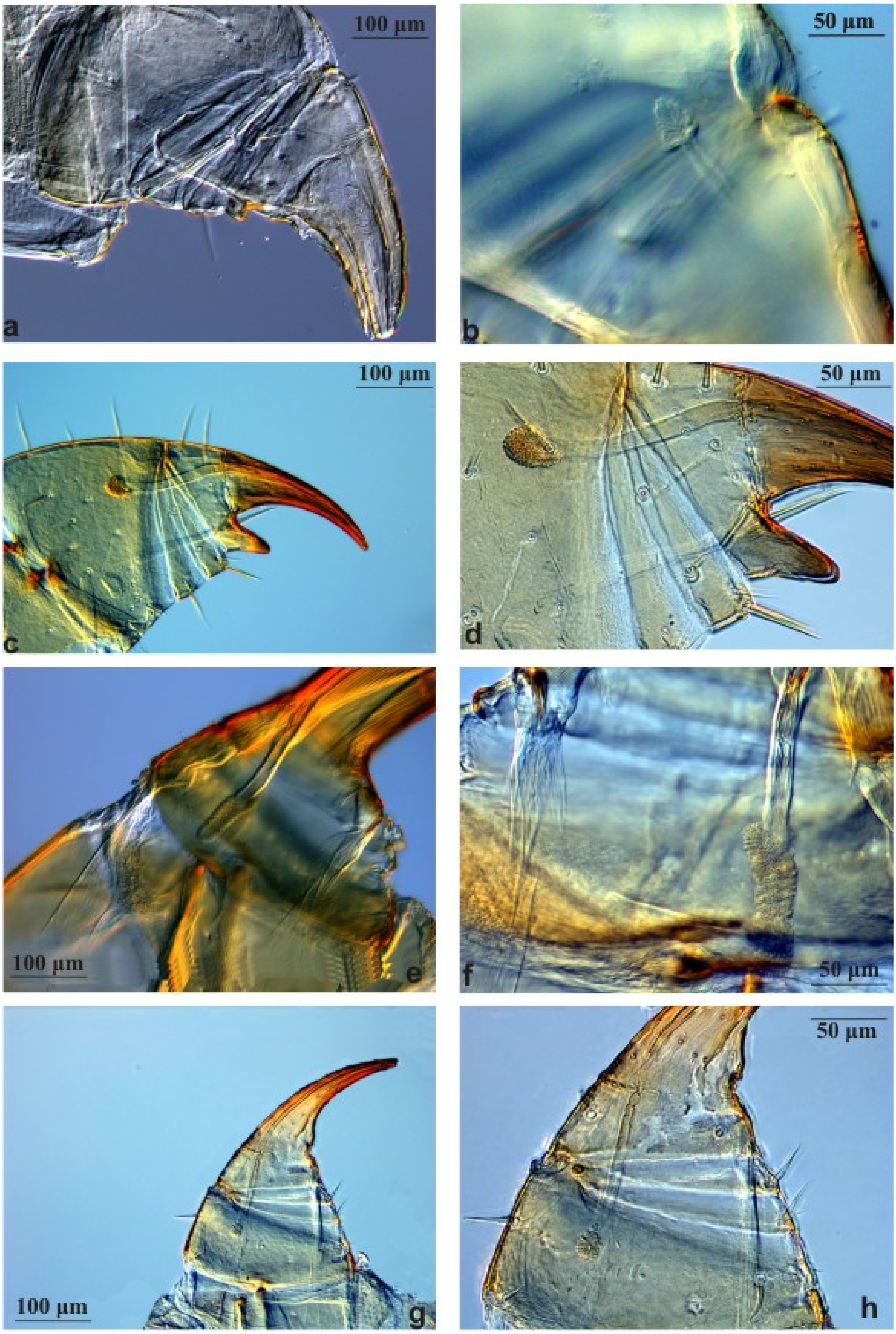


Fig. 7. Poison ducts in Geophilomorpha. DIC images. II. a), b) *Tuoba poseidonis.* c), d) *Strigamia crassipes.* e), f) *Henia bicarinata*. g), h) *Henia illyrica.*

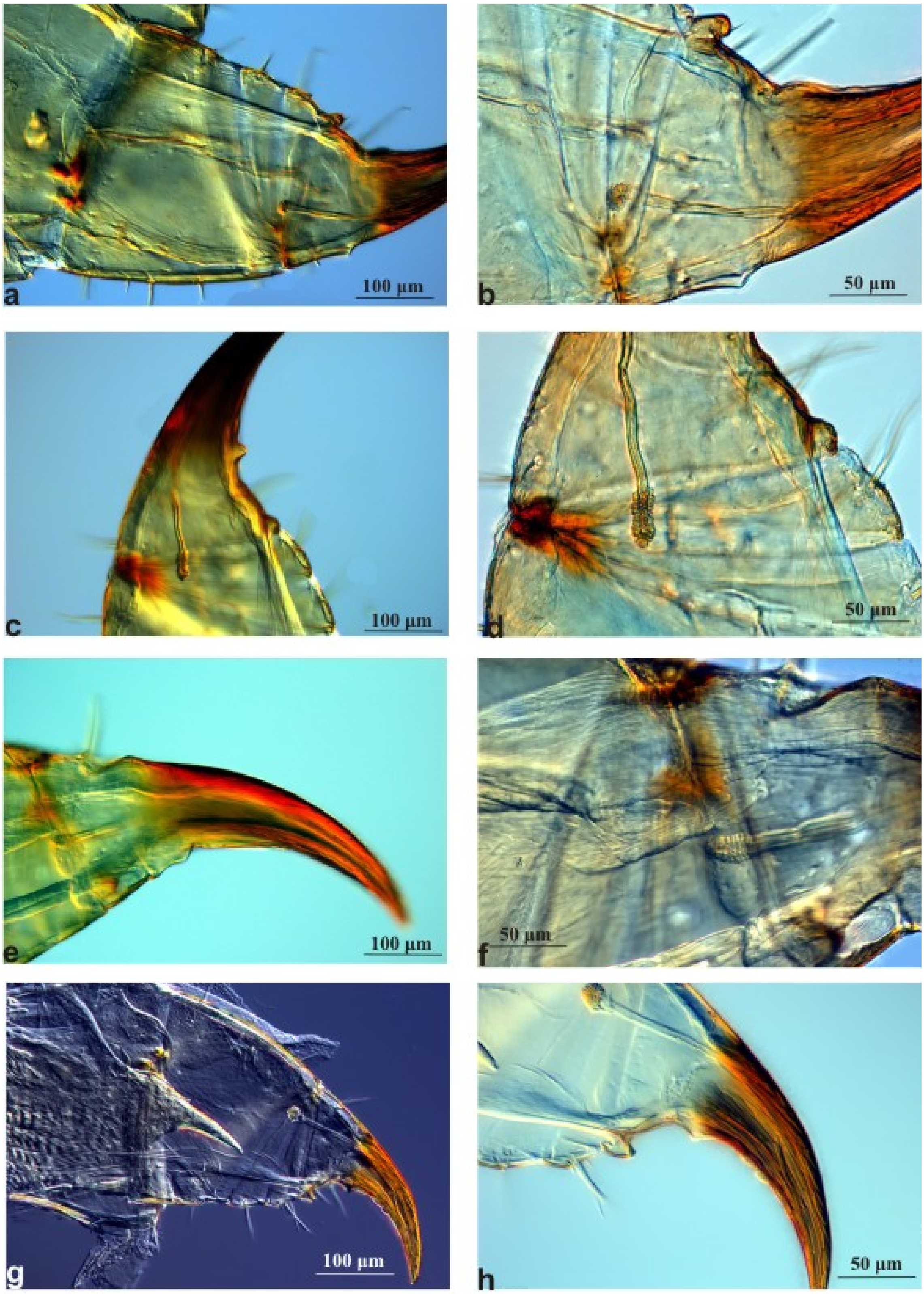


Fig. 8. Poison ducts in Geophilidae. DIC images. III. a), b) *Geophilus alpinus.* c), d) *Geophilus carpophagus*. e), f) *Geophilus flavus*. g), h) *Geophilus truncorum.*

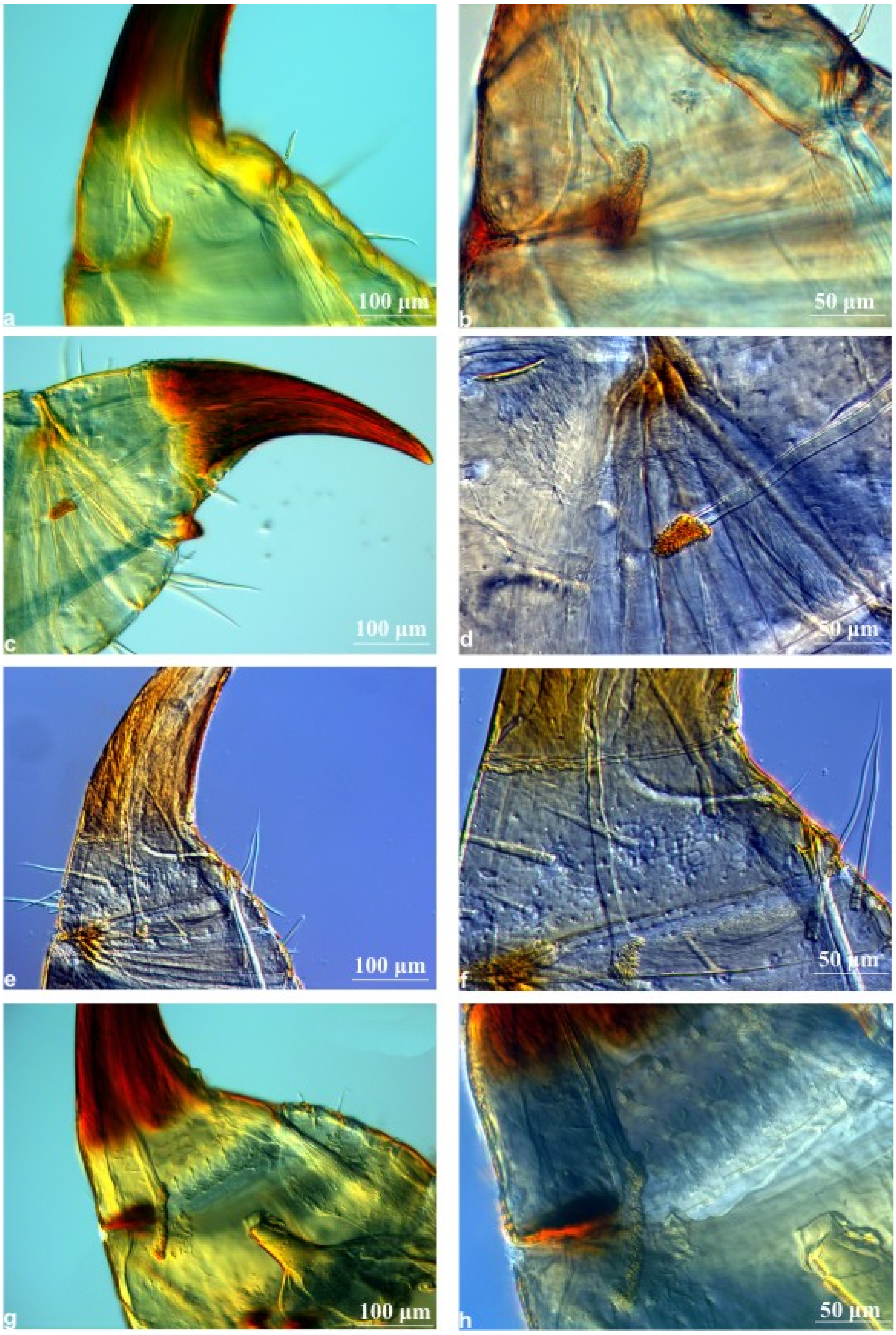


Fig. 9. Poison ducts in Geophilidae. DIC images. IV. a), b) *Clinopodes flavidus.* c), d) *Pachymerium ferrugineum*. e), f) *Pleurogeophilus mediterraneus*. g), h) *Stenotaenia linearis.*

In *Dicellophilus carniolensis* (Mecistocephalidae), the poison duct extends through the tarsungulum, tibia, femur and trocantheroprefemur. The duct is straight and runs in the middle of the forcipulae (fig. 2 a,b). The poison calyx is elongated, cylindrical, with numerous small pores and is symmetrical (figs. 5d, 6 a,b).

In *Stigmatogaster gracilis* (Himantariidae), the poison duct extends into the anterior part of the trochantheroprefemur and runs along the outer edge of tarsungulum for the distal part and then, at the end, within the tarsungulum (fig. 2 c,d); the poison calyx is a symmetrical elongate cylinder but with a few tiny pores only (figs. 5f, 6 c,d).

In *Schendyla nemorensis* (Schendylidae), the duct, running rounded, reaches the tibia; the calyx is symmetrical, lampbrush-like in shape, with the pores surrounding only its base (figs. 2 e, f; 6 e,f).

In Dignathodontidae, shape and position of the calyx differ among the species. In *Henia bicarinata* the duct runs for along the external edge of the tarsungulum most of its length and then is rounded, in the proximal part of the tarsungulum; the calyx is lodged within the tibia and the femur and has a sub-chordate, not symmetrical, shape. (fig 7 e, f). In *Henia iiyrica*, instead, the poison calyx is located within the tronchantheroprefemur and is symmetrical, lampbrush-like in shape, with pores only at the base. (fig.7 g, h); the duct is curved, running in the distal part along the external edge of the ungulum and then in the middle of the tarsungulum. In *Henia vesuviana*, the poison duct extends into the trunk, according to Duboscq (1898) between the 12th and 18th segments: in the specimens examined in this study, runs until the 23th segment and the calyx is symmetrical round shaped; maybe the position of the calyx into the trunk is related to the number of the leg-bearing segments of the specimens.

In *Strigamia crassipes* (Linotaeniidae), the poison calyx is lodged in the tarsungulum, and is an asymmetrical round mass with numerous pore confined to the base of the calyx (fig. 7 c, d). The duct runs rounded from the end of the tarsugulum, where it begins to run in the middle of the forcipula, while it runs along the external edge of the ungulum in the distal part of tarsungulum.

In *Geophilus alpinus*, *Geophilus carpophagus* and *Geophilus flavus* the poison calyx is located in the intermediate articles (tibia and femur) of the forcipula (fig.8 a,b,c,d,e,f). In *Geophilus alpinus* the shape of the poison calyx is round and symmetrical, instead in *Geophilus carpophagus* and *Geophilus flavus* it is sub-cordate and symmetrical. In *Geophilus truncorum*, the poison calyx extends from the femur to the tip of the trochanteroprefemur and is brush-like in shape (fig. 8 g,h). In all these species the duct runs rounded and in *G. carpophagus* and *G. flavus* in the middle of the forcipula, while in *G.*

alpinus and in *G. truncorum* it runs along the external edge in the distal part of the tarsungulum and then in the middle in the proximal part of tarsungulum.

In *Pachymerium ferrugineum, Pleurogeophilus mediterraneus* and *Tuoba poseidonis* the poison calyx extends from the tibia to the femur (figs. 7 a,b and 9 c,d,e,f); in *P. mediterraneus*, the calyx is asymmetrical and lampbrush-like in shape; in *T. poseidonis*, is symmetrical and brush-like and in *P. ferrugineum* it is symmetrical and sub-cordate. In *Clinopodes flavidus* and *Stenotaenia linearis* the shape of the poison calyx is asymmetrical and bell-bottomed, but the position is different: in *C. flavidus* runs from the tarsungulum to the femur (fig. 9 a,b); in *S. linearis*, instead, the poison gland cells are distributed across tarsungulum, tibia and femur, reaching the trochanteroprefemur (fig 9 g,h). In all these species the duct is curved and runs for most of its length along the external edge of tarsungulum and then within the tarsungulum in the proximal part of it, except in *P. ferrugineum* and *P. mediterraneus*, where the duct is straight and runs in the middle of the forcipule for its whole length.

Discussions

According to the length of the venom ducts, the 16 species of geophilomorphs analyzed are different; the shortest one is found in *Schendyla nemorensis*, where it is located in the end of tarsungulum and in tibia. In seven of the species analyzed, the calyx is located in the intermediate articles, tibia and femur (*H.bicarinata, G. alpinus, G. carpophagus, G. flavus, P. ferrugineum, P. mediterraneus, T. poseidonis*). In *C. flavidus*, the calyx extends into tarsungulum, tibia and femur, instead in *G. truncorum*, into femur and trochanteroprefemur. In *H. illyrica* and *S. crassipes* is located in trochanteroprefemur and in *D. carniolensis*, *S. gracilis* and *S. linearis* the calyx reaches all the four articles of the forcipule (tarsungulum, tibia, femur and trochanteroprefemur). In none of species considered the calyx is found in the coxosternum, while in *H. vesuviana* reaches the trunk.

Also the shape of the poison calyx varies in the species taken into account; it can be classify into cylindrical (in Mecistocephalidae and Himantariidae), round (in *H. vesuviana*, Dignathodontidae and *G. alpinus*, Geophilidae), sub-cordate (in *H. Illyrica*, Dignathodontidae and *G. flavus* and *G. carpophagus*, Geophilidae), lampbrush-like (in Schendylidae, *H. bicarinata*, Dignathodontidae and *P. mediterraneus*, Geophilidae), bell-bottomed (in *S. linearis* and *C. flavidus*, Geophilidae) and bush-like (in *G. truncorum* and *T. poseidonis,* Geophilidae).

The phylogenetic position of taxa with different shape of poison calyx can be evaluated, against the consensus phylogeny suggested by morphological analysis performed (manuscript I) and using a scolopendromorph as outgroup (fig.10).

A poison calyx of cylindrical shape is the plesiomorph condition for the whole of the Geophilomorpha. This character changes several times. The condition of lampbrush-like calyx evolved independently in *S. nemorensis, H. bicarinata, P. mediterraneus* from cylindrical, round and sub-cordate respectively; the condition of sub-cordate poison calyx evolved independently in *H. illyrica* and *G. flavus + G. carpophagus + P. ferrugineum* round in the first species, and from an indeterminate status the lineage composing the other three species*;* poison calyx round in shape evolved independently in *H. vesuviana*+ *S. crassipes* and *G. alpinus,* from sub-cordate in the last species and from an indeterminate status in the clade including the other two species. The condition of bell-bottomed poison calyx is evolved one time in the clade including *S. linearis*, *C. flavidus* and *T. poseidonis*, but reverted to the condition of bush-like in shape in *T. poseidonis*, as it did, within the *Geophilus* lineage, in *G. truncorum*.

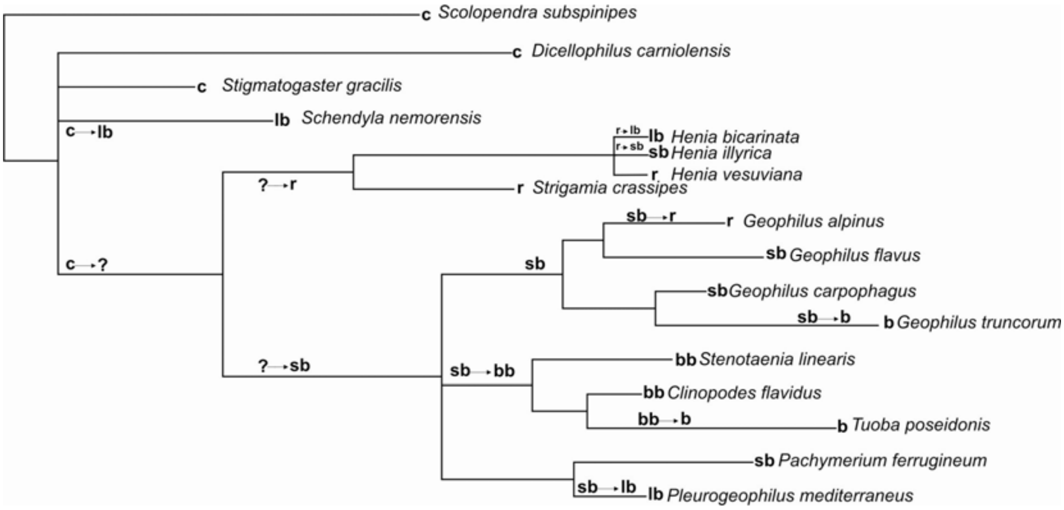


Fig. 10. Evolution of the shape of the poison calyx indicated on the consensus phylogeny obtained with morphological characters (manuscript I). b: bush-like; bb: bell-bottomed; c: cylindrical; lb: lampbrush-like; r: round; sb: sub-cordate.

All chilopods are predatory soil inhabitants and there are adaptations and ecological preferences to special habitats by body construction plans as ecomorphotypes or life-forms. (Voigtländer, 2011). It is possible to evaluate ecological correlates of different shape of poison calyx. Habitat preferences of centipede species have been studied in several European countries, including Italy (Minelli & Iovine, 2007) and the British Isles (Barber, 2005). According to the habitat preferences of the species examined, the different shapes of the poison calyx seem not to be correlate with ecological characteristics (tab. 4)

species	**habitat**	**shape**	
Mecistocephalidae			
Dicellophilus carniolensis	oakwoods	cylindrical	symmetrical
Himantariidae			
Stigmatogaster gracilis	in mediterranean communities and in woodlands both termophilous and mesophilous	cylindrical	symmetrical
Schendylidae			
Schendyla nemorensis	mostly in woodlands both termophilous and mesophilous	lampbrush-like	symmetrical
Dignathodontidae			
Henia (Chaetechelyne) vesuviana	euryecious, frequent in oakwoods	round	symmetrical
Henia (Meinertia) bicarinata	euryecious, rercorded from the seashore	sub-cordate	asymmetrical
Henia (Henia) illyrica	no habitat records avaible	lampbrush-like	symmetrical
Linotaeniidae			
Strigamia crassipes	woodlands	round	asymmetrical
Geophilidae			
Clinopodes flavidus	euryecious, frequent in oakwoods	bell-bottomed	asymmetrical
Geophilus alpinus	euryecious	round	symmetrical
Geophilus carpophagus	euryecious	sub-cordate	symmetrical
Geophilus flavus	euryecious	sub-cordate	symmetrical
Geophilus truncorum	woodlands	bush-like	symmetrical
Pachymerium ferrugineum	euryecious	sub-cordate	symmetrical
Pleurogeophilus mediterraneus	doubtfull ecological significance	lampbrush-like	asymmetrical
Stenotaenia linearis	euryecious	bell-bottomed	asymmetrical
Tuoba poseidonis	seashore, under *Poseidonia*	bush-like	symmetrical

Tab. 4. Habitat preferences and distribution of the species examined.

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Coxal organs in Geophilomorpha: comparative morphology and evolution

Abstract

Geophilomorphs (Chilopoda: Geophilomorpha) are long-bodied animals, with a number of leg-bearing segments ranging between 27 and 191. The last leg-bearing segment is modified in respect to all the preceding ones, as the last legs are not involved in locomotion and their usually swollen coxae, fused to the pleurites to form unitary coxopleura, contain a variable number of coxal organs opening through conspicuous pores on the surface. Number and arrangement of these pores are of great taxonomic importance. Fine-structural investigations demonstrated that coxal organs are lined by pleural transporting epithelia; this suggests that these structures have a osmoregulatory function. Here I studied by different microscopic techniques the topography of the coxal pores and the shape of the cuticular channels leading to them in 15 species of Geophilomorpha. I found a great variation in arrangement, number of the coxal pores and in the shape of the channels. Evolutionary changes of these traits have been reconstructed against the phylogeny of Geophilomorpha and discussed in the light of the ecological preferences of the different species.

Introduction

The coxae of the last pair of centipede legs are often pierced by a variable number of pits, called the coxal pores. The presence of these structure is one of the autapomorphies of Pleurostigmophora (Lithobiomorpha, Scolopendromorpha, Craterostigmomorpha and Geophilomorpha) (Rosenberg et al., 2006).

In Lithobiomorpha each coxa of the last two to five pairs of legs bears ventrally the pore field, into which the pores of the coxal organs open.

In Craterostigmomorpha the inner surface of the two valves of the anal capsule is covered by four pairs of pores fields, separated by broad cuticular bars.

In the Epimorpha (Scolopendromorpha and Geophilomorpha), the sclerite on whose surface these pores open is actually the inflated coxopleuron, that is, an undivided sclerite corresponding to the pleural area of the segment plus the coax of one of the terminal legs.

Originally, these structures were interpreted as the openings of glands, but comparative fine-structural studies showed that the ducts corresponding to the pores are surrounded by transporting epithelia (Rosenberg, 1982, 1983, 1990; Rosenberg and Seifert, 1977 for Geophilomorpha).

The coxal pores in Geophilomorpha, variable in terms of number and arrangement, are an important morphological feature (Eason, 1964): their diversity in number (from one for each coxopleuron to several dozen), size, homogeneity (sometimes with a macropore distinctly larger than the other pores) and arrangement (in some species the pores are distributed over the whole surface of the coxopleura, only on the ventral surface, in other species the pores cover also the dorsal surface of the coxa; in some species, like *Geophilus flavus,* the pores are few in number and situated only ventral in two irregular rows; in other the coxal pores are along the edge of the adjacent metasternite).

The ultrastructure of the coxal pores was studied by transmission electron microscopy, beginning with Rosenberg and Seifert (1977) and Rosenberg (1982).

Coxal organs have a uniform cellular organization. For each coxal pore, a pore channel leads into the coxa; at its base the channel is wider and surrounding by a huge radially arranged ephithelium (Rosenberg, 1982). The main epithelium consists of tall columnar transporting cells; junctional cells and solitary epidermal glands surround this epithelium like a collar; epidermal glands open into the pore canal, which is lined by an undifferentiated epithelium. The main epithelium of the coxal organs displays infoldings of apical and basal cell membrane and plasmalemma-mitochondrial complexes (fig. 1). These traits, characteristic of transport epithelia, suggest that these organs take part in the uptake of water and active ion transport (Berridge and Oshman, 1972).

The coxal organs are thus osmoregulatory organs, excrecting water under wet conditions and absorbing it in dry environments (Rosenberg and Seifert, 1977).

Despite the widespread use of coxal pores in genus- and species-leved diagnoses of geophilomorphs, a systematic comparative topography of the coxal pores in this centipede taxon is still lacking: Rosenberg (1982) described pores in *Stigmatogaster subterraneus*, (Himantariidae), *Strigamia maritima*, (Linotaeniidae), and two members of the Geophilidae: *Stenotaenia linaeris* and *Geophilus flavus* (fig. 2).

A comparative knowledge of the coxal pores is important in a phylogenetic and evolutionary prospective and its ecological relevance needs an adequate assessment.

Here I describe the coxal organs of some geophilomorphs by microscopic techniques never used before in the study of these structures.

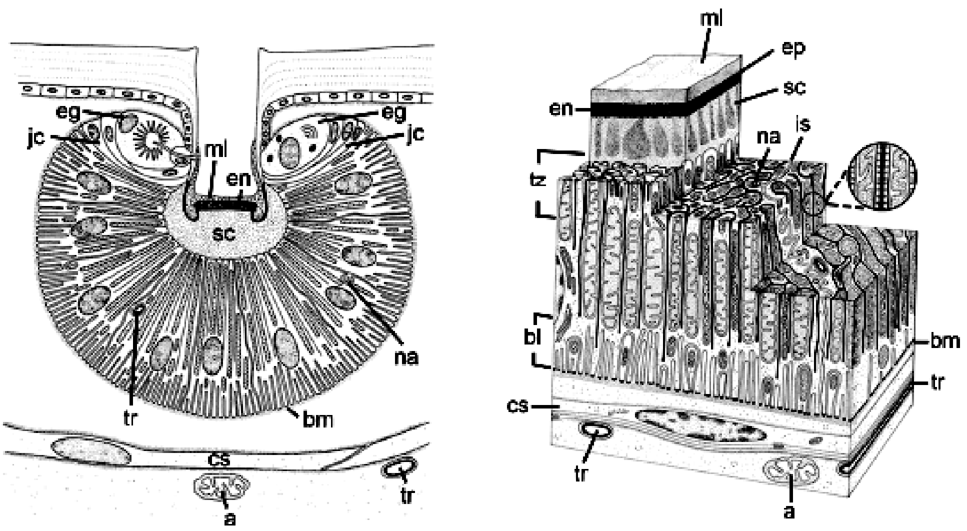


Fig. 1. A Schematic organization of a single coxal organ. B Schematic organization of transport epithelial cells of a coxal organ. Inset: plasmalemma mitochondrial complexes. After Rosenberg (1983), modified by Rosenberg et al. (2011)

a artery; **bl** basal labyrinth; **bm** basal lamina; **cs** cellular sheath; **eg** epidermal gland; **en** endocuticle; **ep** epicuticle; **is** intercellular space; **jc** junctional cell; **ml** mucous layer; **na** neurosecretory axon; **sc** subcuticle; **tr** trachea; **tz** transition zone

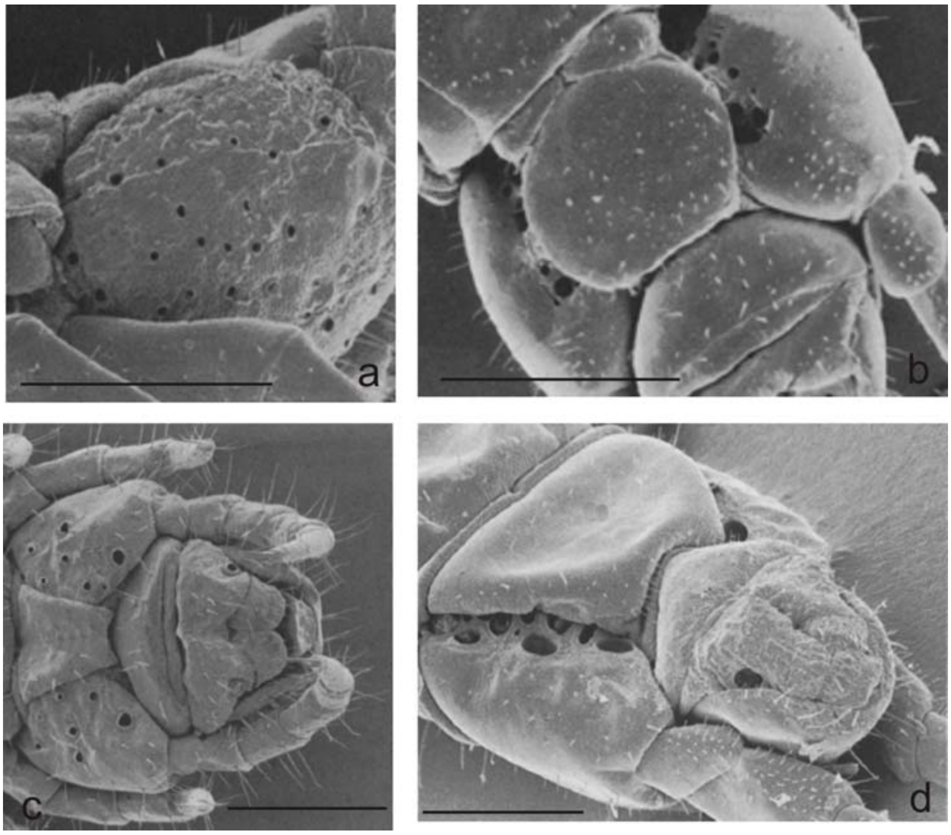


Fig. 2. Coxae of the last leg-bearing segment (Scale bar 100 µm). a) *Stigmatogaster subterranea*, lateral aspect of the coxa of the last leg-bearing segment; b) *Clinopodes linearis*; c) *Strigamia maritima*; d) *Geophilus flavus*. (Rosenberg J., 1982)

Materials and methods

Specimens

The coxal pores of 15 species of Geophilomorpha were examined (tab. 1), belonging to six families: Mecistocephalidae, Himantariidae, Schendylidae, Dignathodontidae, Linotaeniidae, Geophilidae. I collected in the field almost all specimens examined, otherwise I used specimens from to the Minelli-Bonato collection, Dipartimento di Biologia, Università di Padova.

To avoid possible ontogenetic variation, only adult specimens were studied.

Examination

To analyze number, size and arrangement of the coxal pores, all specimens were first examined by light microscopy (Leica DMLB). Then, the terminal part of the trunk of one specimen of each species was dissected out from the trunk. To observe the structure of the coxal pores, internal soft tissues were digested with KOH 5% at 50°C for 24 h at least: this method allowed to remove soft tissues while leaving the exoskeleton intact. The remaining cuticle was bleached with acetic acid, washed with distilled water, then each sample was mounted in glycerol. In the mounting process care was paid to prevent deformation (compression or crushing) using spacers between slide and coverslip. The slides were examined integrating different microscopic techniques, exploiting the effect of the autoflorescence of the cuticle. Specimens were studied with a Leica DM5000B microscope, using bright field light or differential interference contrast (DIC). Pictures were acquired with a Leica DFC 300 FX camera using Leica Application Suite software (version 2.6) and Helicon Focus software. Some digested specimens were also observed with confocal laser scanning microscopy (CLSM) Leica DMI 6000B equipped with a Leica TCS SP5 unit, with 543 nm Helium/Neon laser and 550–680 nm emission filter. Optical sections were taken at a pace of 0.17 lm and analyzed with ImageJ (version 1.42).

Results

Number, size and arrangement of the coxal pores vary among the species considered (tab. 1). The coxopleura bear a few to a large number of pores. These can be scattered all over the ventral surface of the coxopleuron or occur along or under the edge of the metasternite or open into pits (figs. 3-4-5).

The channel of the coxal pores varies in depth and shape: they can be short and wide, straight cylindrical for all the length and the internal base as large as well as the opening of the pore, with uniform diameter; the channel can be otherwise very deep, with the lateral sides parallel for the first part of its length or distinctly bent, with diameter not uniform (tab. 1; figs. 6-7-8).

Coxal pores on the coxopleuron of the ultimate leg			
species	**numbers**	**arrangement**	**channels shape**
Mecistocephalidae			
Dicellophilus carniolensis	more than 20	scattered all over the coxopleuron	cylindrical and short, uniform diameter
Himantariidae			
Stigmatogaster gracilis	more than 20	along the edge of metasternite	cylindrical and long, with not uniform diameter
Schendylidae			
Schendyla nemorensis	2 pores	along the edge of the metasternite	cylindrical and short
Dignathodontidae			
Henia (Chaetechelyne) vesuviana	1 pore+ many pores in pits	at the anterior part of the coxopleuron and along the edge of the metasternite	single pore: short and cylindrical, diameter uniform pores in pits: long and cylindrical, with not uniform diameter
Henia (Meinertia) bicarinata	1 pore+ many pores in pits	at the anterior part of the coxopleuron and along the edge of the metasternite	single pore: short and cylindrical, diameter uniform pores in pits: long and cylindrical, with not uniform diameter
Linotaeniidae			
Strigamia acuminata	10-15 pores	scattered over the coxopleuron	cylindrical and short, uniform diameter
Geophilidae			
Clinopodes flavidus	several pores in 2 pits	at the anterior part of the coxopleuron and along the edge of the metasternite	long and cylindrical, with not uniform diameter
Geophilus alpinus	6 pores	along the edge of the metasternite	cylindrical and short, uniform diameter
Geophilus carpophagus	4 pores	along the edge of the metasternite	cylindrical and short, uniform diameter
Geophilus flavus	6 pores	along the edge of the metasternite	globular with not uniform diameter
Geophilus osquidatum	3 pores	along the edge of the metasternite	cylindrical and short, uniform diameter
Geophilus truncorum	2 pores	along the edge of metasternite	cylindrical and short, uniform diameter
Pleurogeophilus mediterraneus	more than 20	over the whole coxopleura	shallow and cylindrical
Stenotaenia linearis	several pores in 2 pits	at the anterior part of the coxopleuron and on the coxopleuron	long and cylindrical, with not uniform diameter
Tuoba poseidonis	several pores in 2 pits	at the anterior part of the coxopleuron and on the coxopleuron	long and cylindrical, with not uniform diameter

Tab. 1. Coxal pores of the last leg in the 15 species considered in this study

In *Dicellophilus carniolensis* (Mecistocephalidae), the coxal pores are distributed over the entire surface of the coxopleuron, small and very numerous with one larger coxal pore (the macropore) in the middle of the mass of smaller ones (figs. 3a-5a); the channel varies in shape and depth: the smallest pores have cylindrical and short channels, the macropore and some larger pores, instead, are very deep and with not uniform diameter, narrowing towards the end of the channel, then expand (fig. 6a-b). The macropore is the only coxal pores present at hatching and remain the largest ones throughout growth, the other pores open later and increase in number (Bonato et al. 2010).

In *Stigmatogaster gracilis* (Himantariidae), the coxal pores open into a long pit along the whole edge of the adjacent metasternite (fig, 3b); the channels of the coxal pores are long with not uniform diameter, with a constriction and final enlargement (fig. 6c-d).

In *Schendyla nemorensis* (Schendylidae) there are two coxal pores on each side, along the edge of the adjacent metasternite, with a large opening, shallow and with cylindrical channels, of uniform diameter (fig. 6l).

In *Henia vesuviana* (Dignathodontidae) there are one large pore adjacent to the metasternite and several small pores opening into a pit at the anterior base of the coxopleuron (figs. 3c-5b); the shape of the single pore is cylindrical, not particularly deep, of uniform diameter; the small pores, instead, have a deeper channel of not uniform diameter (fig. 6e-f).

In the other dignathodontid studied, *Henia bicarinata* the pattern of the coxal pores is the same as in *Henia vesuviana*: a macropore adjacent to the metasternite and the others pores opening into a pit (fig. 3d); in this case, the shape of the pores are similar: all the pores are cylindrical, with almost constant diameter (fig. 6g-h).

In *Strigamia acuminata* (Linotaeniidae) the coxal pores are ten to fifteen, open directly onto the surface and are distributed on the coxopleuron. The channels are more or less deep, but always cylindrical with the same diameter from the opening to the base and parallel lateral sides (fig. 6i).

In the species of *Geophilus* (Geophilidae) the coxal pores of the last legs open directly onto the surface, mostly along the edge of the metasternite (fig. 4 a-b-c-d).

In *Geophilus alpinus* four to seven coxal pores are clustered along the edge of the adjacent metasternite; the pores are cylindrical, quite deep, of uniform diameter (fig. 8a-b).

In *Geophilus carpophagus* the coxopleuron presents four to eight coxal pores; the channels are quite deep and the lateral sides are convergent posteriorly, almost straight (fig. 8c-d).

In *Geophilus flavus* there are six to ten pores opening along the edge of the metasternite; the shape of the channel is globular, with not parallel and rounded lateral sides (fig. 8e-f).

In *Geophilus osquidatum* two to four pores on each coxopleuron are adjacent to the edge of the metasternite (fig 8 i-l); the channels of the pores are wider than long, of uniform diameter; the two pores in *Geophilus truncorum* are in the same condition (figs. 5d, 8g-h).

In *Pleurogeophilus mediterraneus* (Geophilidae) coxal pores are uniformly small and very numerous and open individually onto the surface (figs. 3h, 5c); the channels are shallow and cylindrical (fig. 7c-d).

In *Clinopodes flavidus*, *Tuoba poseidonis* and *Stenotaenia linearis* (all geophilids) the coxal pores open into pits (fig. 3e-f-g); the channels are longer than wide, of not uniform diameter: all of them show a narrowing towards the end, the base is globular and sometimes wider than the opening of the pore (fig. 7a-b-g-h-e-f).

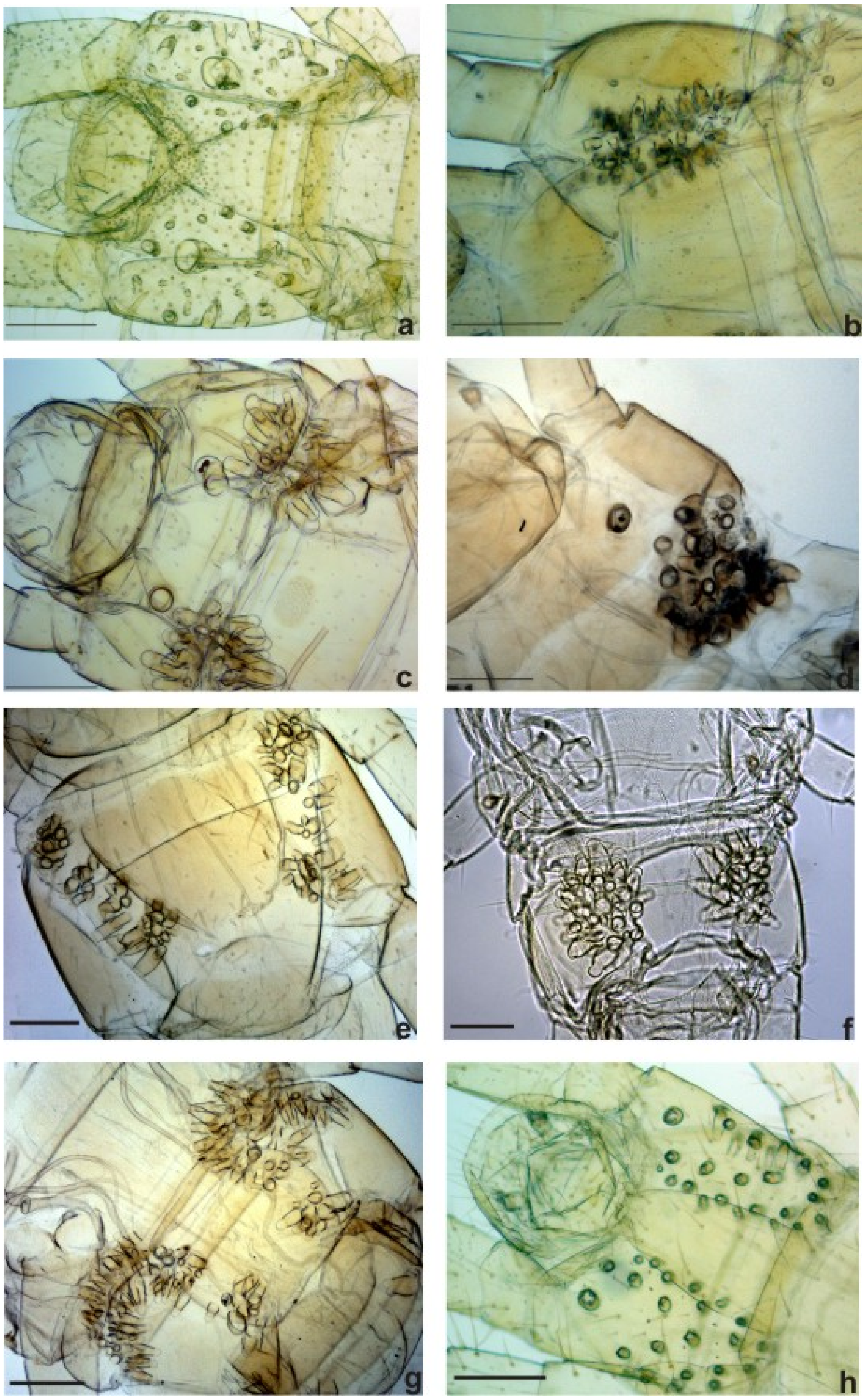


Fig. 3. Coxopleura and coxal pores of the ultimate legs, LM images. I. a) *Dicellophilus carniolensis*; b) *Stigmatogaster gracilis*; c) *Henia vesuviana*; d) *Henia bicarinata*; e) *Clinopodes flavidus*; f) *Tuoba poseidonis*; g) *Stenotaenia linearis*; h) *Pleurogeophilus mediterraneus*. Scale bar 200 μm.

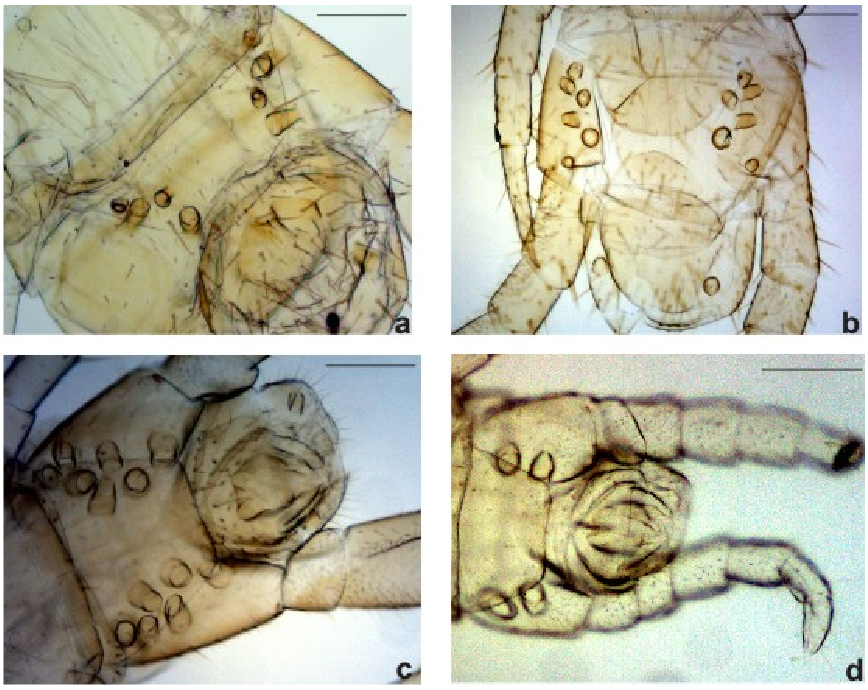


Fig. 4. Coxopleura and coxal pores of the ultimate legs, LM images. II: a) *Geophilus carpophagus*; b) *Geophilus alpinus*; c) *Geophilus flavus*; d) *Geophilus truncorum*. Scale bar 200 µm.

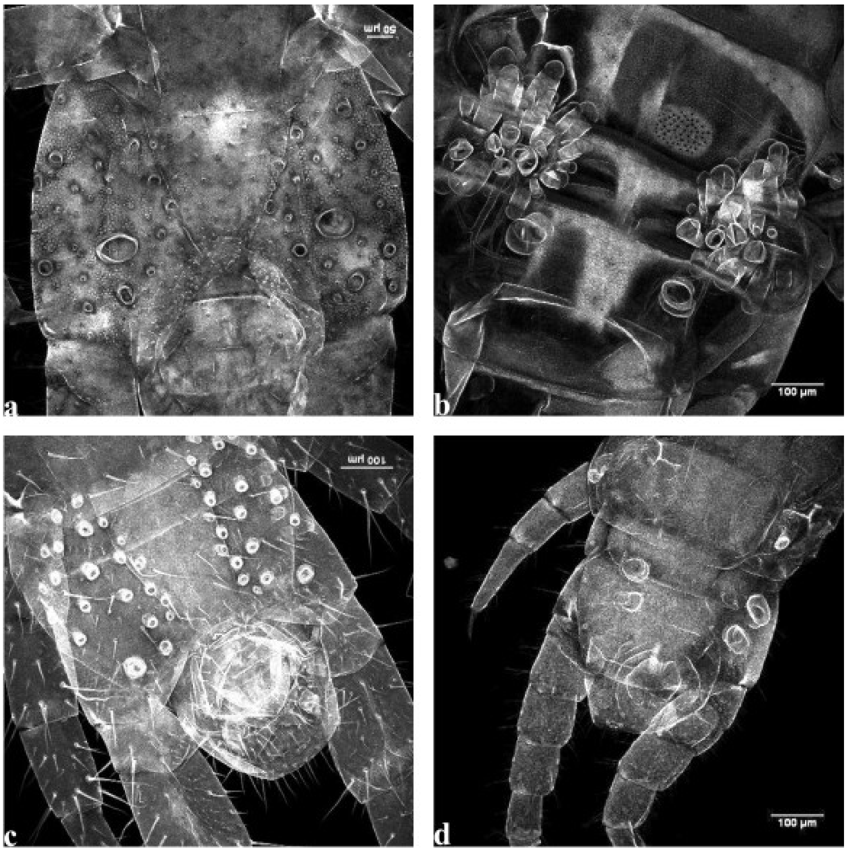


Fig. 5. Coxopleura and coxal pores of the ultimate legs, CLSM images. a) *Dicellophilus carniolensis*; b) *Henia vesuviana*; c) *Pleurogeophilus mediterraneus*; d) *Geophilus truncorum*.

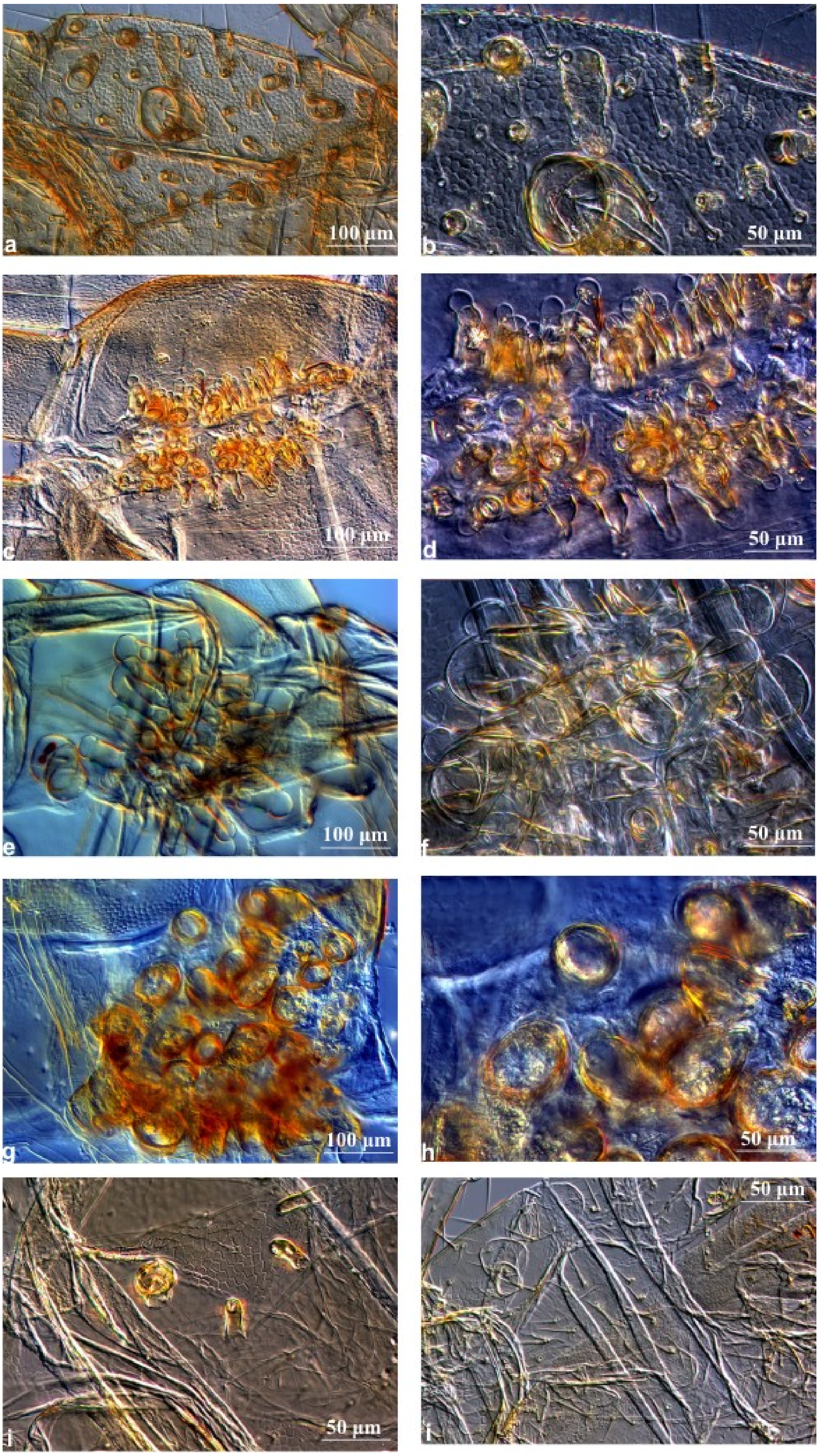


Fig. 6. Coxal pores of Geophilomorpha, DIC images. I. a)-b) *Dicellophilus carniolensis*; c)-d) *Stigmatogaster gracilis*; e)-f) *Henia vesuviana*; g)-h) *Henia bicarinata*; i) *Strigamia acuminata*; l) *Schendyla nemorensis.*

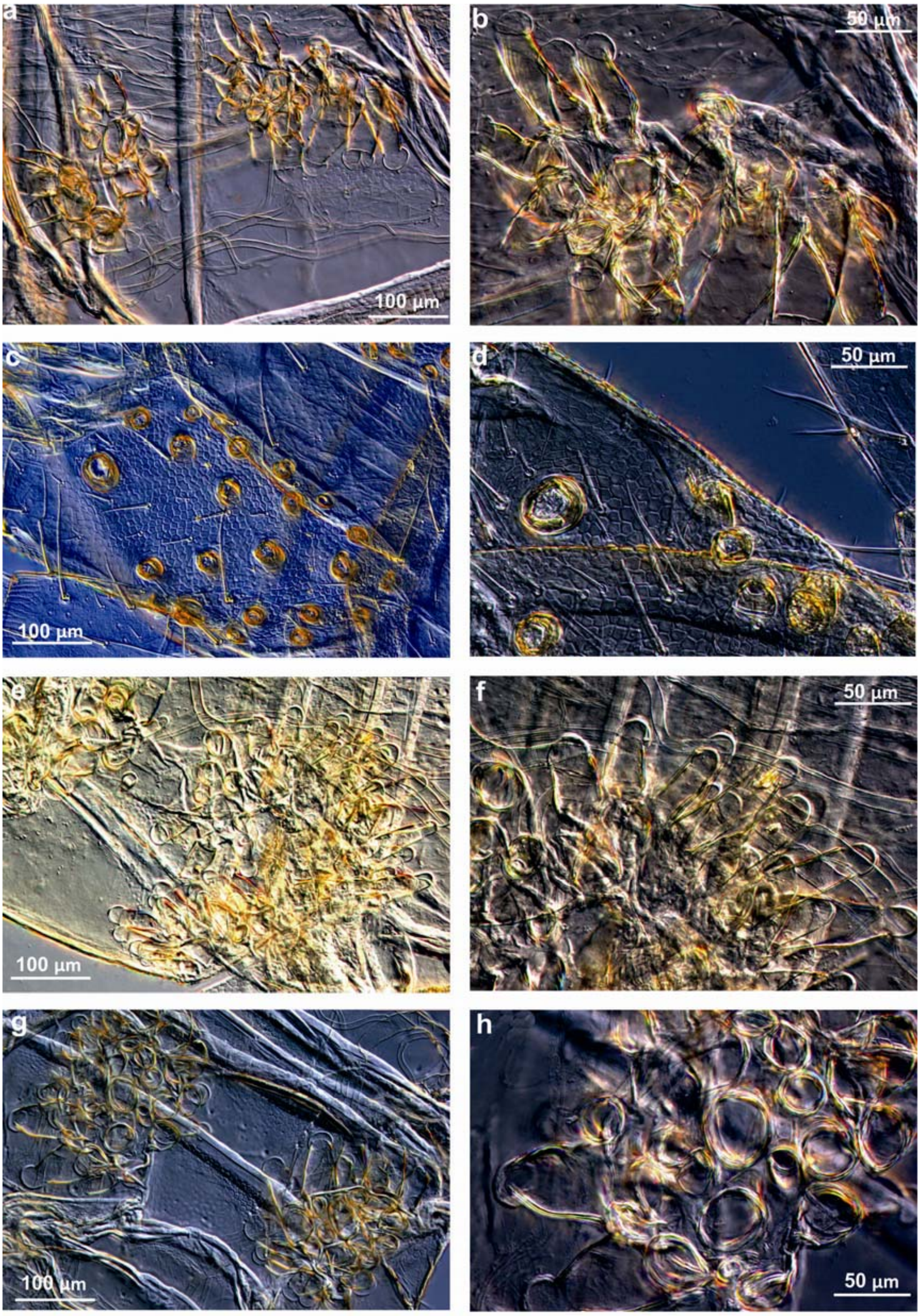


Fig. 7. Coxal pores of Geophilomorpha, DIC images. II. a)-b) *Clinopodes flavidus*; c)-d) *Pleurogeophilus mediterraneus*; e)-f) *Stenotaenia linearis*; g)-h) *Tuoba poseidonis.*

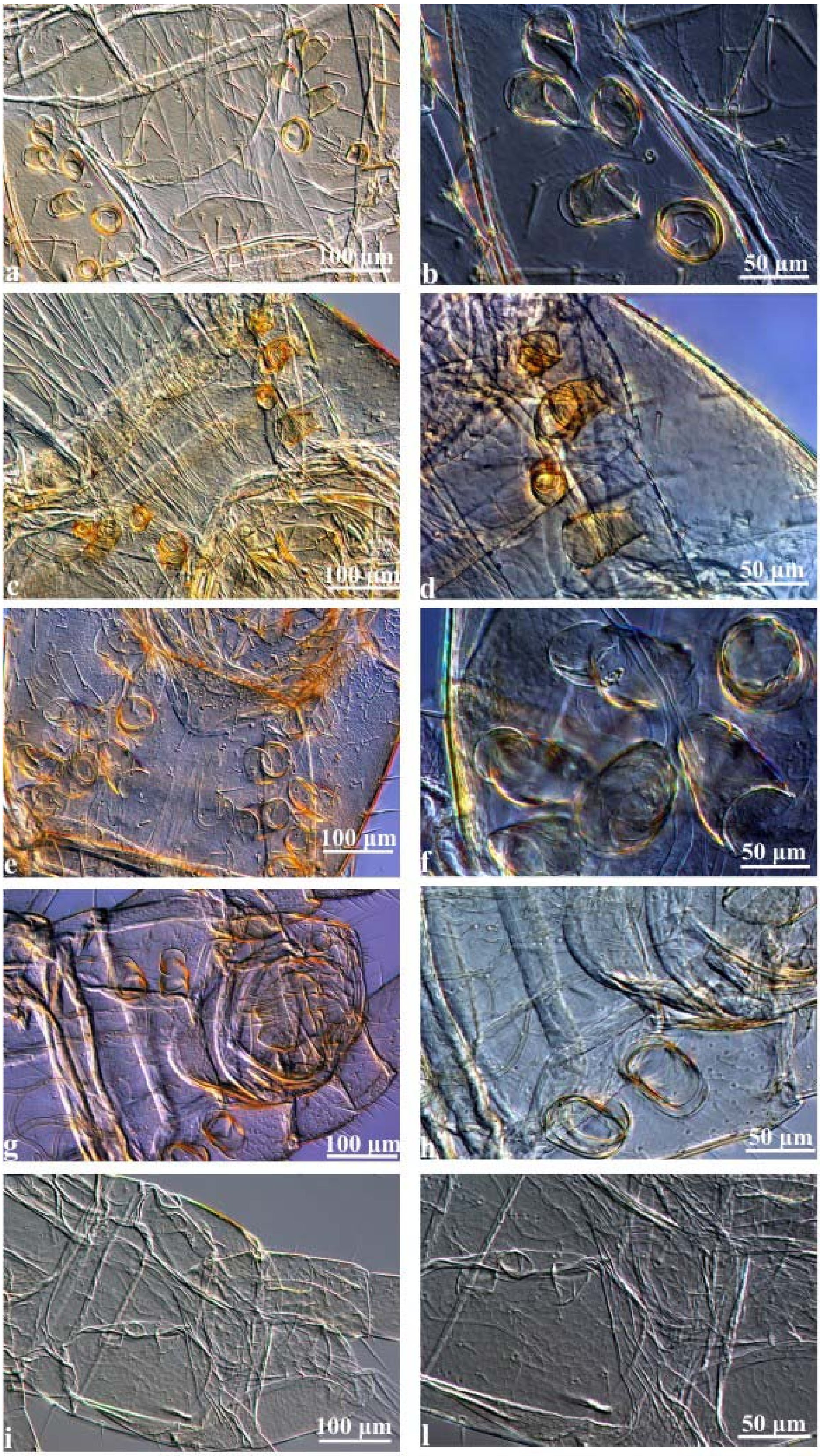


Fig. 8. Coxal pores of Geophilomorpha, DIC images. III. a)-b) *Geophilus alpinus*; c)-d) *Geophilus carpophagus*; e)-f) *Geophilus flavus*; g)-h) *Geophilus truncorum*; i)-l) *Geophilus osquidatum*,

Discussion

In the Geophilomorpha, the coxopleuron of the ultimate pair of legs bears a various numbers of coxal pores, the appearance of which is importance in routinary species identification.

A comparative examination by complementary microscopical techniques of the coxal pores in different species of geophilomorphs reveals a great diversity in the arrangement and number of the pores and in the and shape of the channels opening through them.

The coxal pores are either distributed over the entire surface the coxa (*D. carniolensis*, *P. mediterraneus*, *S. acuminata*), or concentrated along the edge of the adjacent metatergite (all the species analyzed of the genus *Geophilus, Schendyla nemorensis*), or open into pits at the anterior part of the coxopleuron (H. *vesuviana*, *H. bicarinata*, *Stenotaenia linearis*) or adjacent to the metasternite (*Stigmatogaster gracilis*, *T. poseidonis*, *C. flavidus)*.

The shape of the channels of coxal pores varies among these species: the channel of the coxal pores opening directly onto the surface are cylindrical, less or more deep, of uniform diameter or narrowing internally, at the base rounded, as wide as the opening, or less.

The channel of the coxal pores opening into pits are deep, with diameter uniform for most of its length, towards the end there is a constriction, at the end the channel is finally enlarged in a rounded shape, usually wider than the opening of the pore.

The different arrangement of coxal pores found in the different species can be evaluated against a consensus phylogeny suggested by a morphological analysis performed and using as outgroup a scolopendromorph (manuscript I) (fig. 9).

For the whole of the Geophilomorpha, numerous coxal pores opening directly onto the surface of the coxopleuron of the ultimate legs is the plesiomorph condition, shared with the sister taxon, the Scolopendromorpha. This character changes twice. A transition leads to a condition in which coxal pores open into pits on the surface of the coxopleuron or on the adjacent sternite. Another transition leads to a condition in which coxal pores are aggregated and close to the adjacent metasternite.

The condition with coxal pores opening into pits evolved independently in *Stigmatogaster gracilis*+*H. vesuviana*, and in the cluster of *Stenotaenia linearis*+*T.poseidonis*+*C. flavidus*.

The condition with few coxal pores opening directly onto the surface of the coxopleuron and distributed along the margin of the metasternite evolved independently in the cluster of the *Geophilus* and in *Schendyla nemorensis* and *Strigamia acuminata.*

Intersting is *P. mediterraneus* which is the only specie in the sample studied here, that re-evolved the ancient character state.

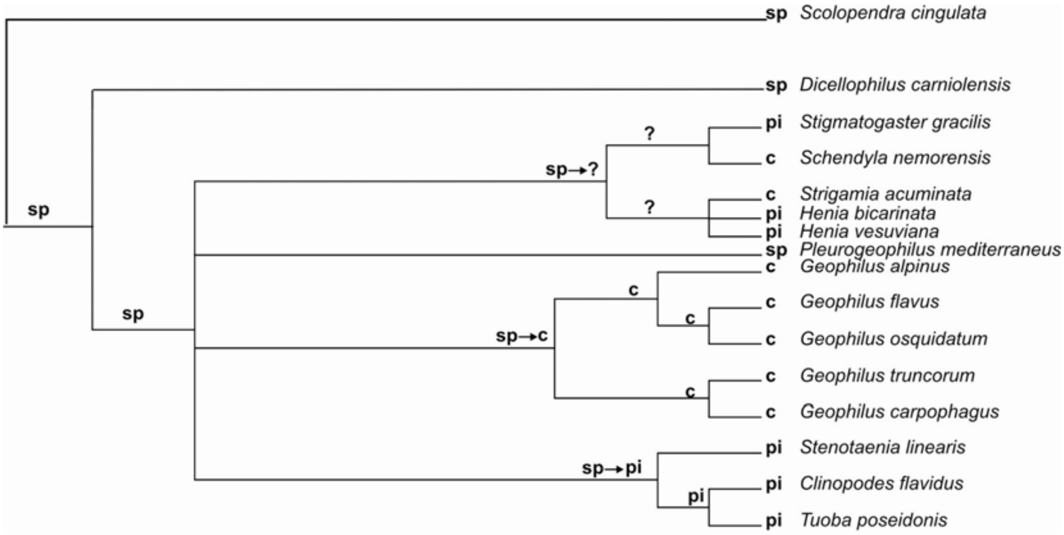


Fig. 9. Evolutionary transitions in the arrangement of the coxal pores of the last legs read against a consensus phylogeny obtained with morphological characters (manuscript I). **c** coxal pores few in number open directly onto the surface adjacent to the metasternite; **pi** coxal pores open into pits on the coxopleura or adjacent to the metastenite; **sp** coxal pores numerous scattered and open directly onto the surface of the coxopleura;

As mentioned in the introduction, the function of coxal organs is osmoregulation (Rosenberg and Seifert, 1977).

All chilopods are predatory soil inhabitants that avoid light and show distinct preference for moist microhabitats. Their habit is generally under stones, bark and leaf litter or inside the soil. Ecological preferences and adaptations to special habitats are mirrored by body construction plans as ecomorphotypes or life-forms. The most important abiotic factor influencing centipede distribution is humidity (Voigtländer, 2011).

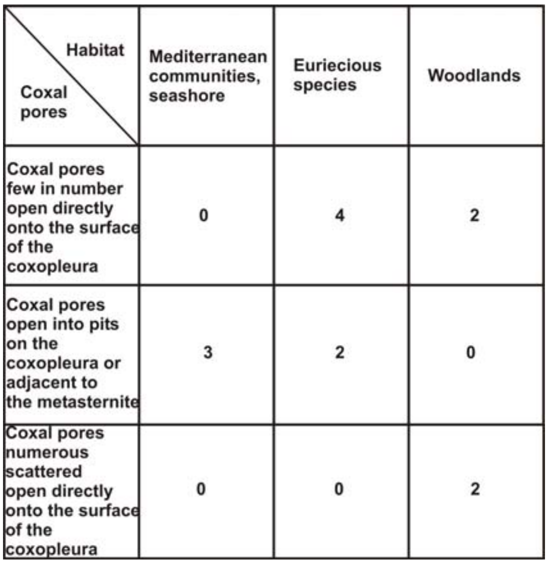
The difference among the species in number and arrangement of coxal pores are possibly related to the different environments colonized by the species analyzed (Verhoeff, 1928).

Habitat preferences of centipede species have been studied in several European countries, including Italy (Minelli & Iovine, 2007) and the British Isles (Barber, 2005) (tab. 2).

According to the habitat preferences of the species examined, the different number and arrangement of the coxal pores seem to be correlate with ecological characteristic (tab. 3).

species	habitat	coxal pores
Mecistocephalidae		
Dicellophilus carniolensis	oakwoods	numerous pores, scattered all over the coxopleuron
Himantariidae		
Stigmatogaster gracilis	in Mediterranean communities and in woodlands both thermophilous and mesophilous	into pits, along the edge of metasternite
Schendylidae		
Schendyla nemorensis	mostly in woodlands both thermophilous and mesophilous	few pores, along the edge of the metasternite
Dignathodontidae		
Henia (Chaetechelyne) vesuviana	euriecious, especially frequent in oakwoods	into pits, at the anterior part of the coxopleuron and along the edge of the metasternite
Henia (Meinertia) bicarinata	euriecoius, recorded from the seashore	into pits, at the anterior part of the coxopleuron and along the edge of the metasternite
Linotaeniidae		
Strigamia acuminata	woodlands	few pores, scattered over the coxopleuron
Geophilidae		
Clinopodes flavidus	euriecious species , oakwoods	into pits, at the anterior part of the coxopleuron and along the edge of the metasternite
Geophilus alpinus	euriecious	few pores, along the edge of the metasternite
Geophilus carpophagus	euriecious, mostly from woodlands	few pores, along the edge of the metasternite
Geophilus flavus	quite euriecious	few pores, along the edge of the metasternite
Geophilus osquidatum	mostly in woodlands both thermophilous and mesophilous	few pores, along the edge of the metasternite
Geophilus truncorum	woodlands	few pores, along the edge of the metasternite
Pleurogeophilus mediterraneus	doubtfull ecological significance	numerous pores, over the whole coxopleura
Stenotaenia linearis	euriecious	into pits, at the anterior part of the coxopleuron and on the coxopleuron
Tuoba poseidonis	seashore, under *Poseidonia*	into pits, at the anterior part of the coxopleuron and on the coxopleuron

Tab. 2. Habitat preferences and distribution of the species examined and the different arrangement and number of coxal pores of the last leg-bearing segment.



Habitat Coxal pores	Mediterranean communities, seashore	Euriecious species	Woodlands
Coxal pores few in number open directly onto the surface of the coxopleura	0	4	2
Coxal pores open into pits on the coxopleura or adjacent to the metasternite	3	2	0
Coxal pores numerous scattered open directly onto the surface of the coxopleura	0	0	2

Tab. 3. Correlation between habitat preference of the species examined and the coxal pores of the last leg-bearing segment.

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